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CONTRIBUTIONS TO THE FOREBRAIN MORPHOLOGY IN AMPHIBIANS

BY

GERTIE SÖDERBERG
LIC. PHIL.

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CONTRIBUTIONS
TO THE FOREBRAIN MORPHOLOGY
IN AMPHIBIANS

DISSERTATION
FOR THE DOCTORATE

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STOCKHOLM
ALB. BONNIERS BOKTRYCKERI
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BY

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(From the Zootomical Institution; University of Stockholm.)

With 29 figures in the text.

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HISTORICAL.

A considerable number of investigators have during the last decades of the 19th century studied the amphibian brain. The earlier of these investigators (among whom we may name STIEDA 1875; OSBORN 1883, 84, 87, 88; KÖPPEN 1888; BURCKHARDT 1891) have as a rule studied the brain as a whole, and only touched on the more general features of the morphology of the forebrain. An interesting fact in reference to recent brain research, is that OSBORN, by his conception of the dorsal commissure in the commissural-bed of the telencephalon as a corpus callosum, indicates that he considers the area from which these callosal fibres emerge to be a cerebral cortex. He also terms a cell-party connected with the upper part of commissura anterior, corpus striatum, a nucleus which he later points out as lacking in urodeles.

KÖPPEN, who has protested against OSBORN's corpus striatum in Rana being homologous with that of other vertebrates, has also attempted to determine the position of this nucleus in the frogbrain. He proposes to assign the name striatum to a nucleus situated immediately before the bundle of Meynert in diencephalon acknowledging at the same time, however, that he is unable to decide the question of its position. Köppen was the first to attempt to divide the telencephalon in the Amphibia into a dorsal and a ventral part. He lays the boundary between these two parts through zona limitans medialis, the medial and the lateral ventricular groove and under the laterally descending cell-wedge; the ventral part consisting only of that part of the telencephalon lying in front of the commissural-bed, caudal to which the dorsal part alone is found.

Edinger's work "Das Vorderhirn" (1888) contains a somewhat more detailed account of the forebrain of the Amphibia, which here, as in the other vertebrates, he divides into two parts: the "Mantel" and the "Stammganglion" or corpus striatum. He mentions no boundary between these two parts of the telencephalon. That part of the brain-wall which in amphibians extends basally and laterally he defines as the stammganglion, the remaining portion would thus constitute the mantle. To the latter he also assigns the epithelial membrane, which unites the two hemispheres above and behind foramen monroi. Edinger points out that the wall of the ventricle consists, as is the case in embryons of all vertebrates, of two layers, an inner one formed of cells, and an outer one of fibres and glia. According to Edinger, no trace of cerebral cortex can be found. The amphibian brain would thus remain at the embryonic stage. The differentiations noticeable in a couple of spots in the ventricular cell-layer, may possibly be rudiments of future ganglia. Homologies to the various parts of the telencephalon in other vertebrates are lacking, except in a single case, where he believes he has discovered an homology to the ammons-formation of reptiles. That part of the mantle described as the spot where, in reptiles, a clearly defined ammons-formation is later to be found, is moreover illustrated on a horizontal section of a frogbrain. Both description and illustration prove that Edinger here speaks of the nucleus lateralis septi.

Edinger conceives the amphibian brain to be of a particularly primitive type: "Das Amphibiengehirn ist das einfachste Gehirn, welches in der Vertebratenreihe vorkommt." — "So ausserordentlich einfach ist das Gehirn bei allen den oben aufgezählten Amphibien gebaut. Es erfährt auch von der letzten Zeit des Larvenlebens an bis in das Alter des Tieres keinerlei Vervollkommnung mehr." Edinger somewhat alters this conception, however, in a paper published later (1893). He has by comparing the conditions in dipnoans arrived at the conclusion that a cerebral cortex, even of a rudimentary character, is to be found in the Amphibia as well. A number of histological investigations of the forebrain of Amphibia carried out by Oyarzun, Cajal and Bellonci have contributed to Edinger's conception of the caudal part of the mantle as an olfactory cortex. He does not however appear to have made any recent investigations of the amphibian forebrain; there is nothing in the text to explain why he chose the expression "rudimentary" in reference to the cerebral cortex of the same.

Mrs Gage (1893) could not find any homology to the ammons-formation in the brain of Diemictylus investigated by her. She contents herself with naming the medio-dorsal wall: the callosal eminence, and points out, at the same time, that it is only slightly developed at the larval stage. Mrs Gage defines the area confined within the laterally descending cell-wedges and the ventricular cells, as striatum.

The first to publish a more detailed description of the telencephalon of Amphibia was Cajal (1896). He treats in this paper of morphological as well as histological conditions. Unfortunately, the appellations of the various parts of the forebrain are as a rule not very well chosen, and show that Cajal's conception of the forebrain of the frog is partly based on erroneous homologies. He calls the part lying dorsal to zona limitans medialis "septum", and states that it corresponds to the "lame du fornix" of reptiles; while the medio-ventral together with the latero-ventral part is on the other hand defined as the ganglion basale or striatum. The part on the medial side of the ventricle, within the nucleus termed "ganglion basale", Cajal calls epistriatum, homologizing it with the laterally situated epistriatum of reptiles. The boundary between the dorsal part of the cerebral cortex and the ventral striatum Cajal locates at the descending cell-part on the lateral side of the brain named by him "région courbe". Medially he draws the boundary between corresponding parts through zona limitans medialis; the "septum" and the dorso-lateral cortex are assigned to the ammons-formation, on account of their fibre-connections, in spite of the septum having been previously homologized with "septum lucidum".

Gaupp (1897) has published a long and particularly exhaustive description of the telencephalon and its parts in Rana. He divides the hemispheres by means of zona limitans medialis and regio curva (Cajal) into a pallial and a subpallial portion. Gaupp calls the ventro-lateral part only ganglion basale, the medio-ventral on the other hand, being designated septum and ganglion mediale septi; between these lies a cell area, which he calls pars angularis. Gaupp sees in this part a possible homology to that called by Edinger area olfactoria in reptiles. The dorsal and medial part of the pallium are considered as corresponding with the ammons-cortex in other vertebrates. The appellations bestowed by Gaupp on the grooves constituting the boundaries between the different parts of the telencephalon are rather unhappily chosen. This is pointed out by Elliot Smith (1903), who cites as example the name fovea limbica for the groove separating the olfactory bulbs from the hemispheres in Rana, this name in reptiles designating a basal groove, which Smith homologizes with vallecula Sylvii in mammals. Medially between the hemispheres at the border of zona limitans medialis we find a faint sulcus called by Gaupp fissura arcuata; the groove bearing this appellation in reptiles and mammals does not run ventrally to primordium hippocampi, and consequently does not there form the boundary between the pallial and subpallial parts; the correct name for the above-mentioned sulcus in Amphibia would be that proposed by HERRICK (1910) fissura limitans.

Although it is only cursorily that ELLIOT SMITH treats of the amphibian brain in his paper: Cerebral Commissures in the Vertebrata (1903), a number of new views nevertheless comes to light in it on this subject. The part passing under the designation of ammons-formation, he calls primordium hippocampi in amphibians, homologously to the case of other vertebrates; while, in connection with this, he calls the pallial commissure, commissura hippocampi. The medial part of the subpallium is named the paraterminal body instead of septum. ELLIOT SMITH considers it probable that the primordium hippocampi in the Ichtyopsida may be merely the specialized upper part of the primitive paraterminal body.

It is surprising how little known is SNESSAREW's paper: Über die Nervenfasern des Rhinencephalons beim Frosche (1908). He describes in it a number of previously unknown tracts, which should be of importance for the general morphology of the forebrain in Amphibia, and especially for its comparative anatomy. SNESSAREW points out that ventral to the hind part of the lateral ventricle a small crescent-shaped fissure, surrounded by ependymal cells, is to be found, this formation he considers to be a lower horn of the lateral ventricle. The nucleus enclosed by these "ependymal cells" is that which HERRICK has later named the amygdala. The ependymal cells are probably only ordinary ganglion cells, whose dendrites point in one direction; the appearance of a fissure-like formation seems to be a result of fixation, since it does not always appear. If this lower horn really were a part of the lateral ventricle, it would be connected with it at the embryonic stages, which is, however, not the case.

KAPPERS (1908) calls the dorso-medial part of the hemispheres archipallium or primordium hippocampi, this being a more differentiated part of the original paleopallium; no clear boundary can be found between this lateral paleopallium and the medial archipallium. KAPPERS connects the origin of this differentiated cerebral cortex with a diminution of the medial olfactory radiation, causing development of the archipallium into a tertiary end station for the olfactory fibres emerging from the septum. — The part of the septum lying in front of commissura anterior is called by KAPPERS, area precommissuralis septi, while that which stretches dorsally and caudally to foramen monroi is pars fimbrialis septi. KAPPERS refers to striatum as follows: "Ein Corpus striatum ist als solches kaum ausgebildet, was wieder in Übereinstimmung ist mit dem Verhalten bei den Cyclostomen und wie dort zusammengeht mit einer grossen Entwicklung der lateralen und dorsalen Wände." — Corresponding to his appellations for the pallium, KAPPERS introduces, in a paper published the same year on the Phylogeny of Corpus Striatum, the terms paleostriatum and neostriatum. The paleostriatum is to be found in all vertebrates; the neostriatum appears first in reptiles, in which an archistriatum or secondary epistriatum is also found, but must not be confounded with the primary epistriatum of bony fishes, in which it assumes the functions of the paleopallium. Thus amphibians have only a paleostratium. — In this latter paper KAPPERS also lays stress on the fact that the amphibian brain is only at an embryonic stage.

FANNY FUCHS (1908) has investigated Rana temporaria and describes the development of the forebrain; we do not, however, find any more detailed description of the telencephalon. Her conception of its development is sharply criticized by JOHNSTON (1909). Neither does the description she gives of the development of the olfactory bulbs seem to be in accordance with facts, see for example her statement that the first bridge between the bulbs has no connection with the olfactory formation, and further, that the accessory bulbs are the earliest portions of the same.

EDINGER (1908) declares that an epistriatum has certainly been proved as existant in amphibians amongst others, and writes as follows on the position of the same: "Das Epistriatum liegt dem Stammganglion nicht auf, sondern lateral an." The epistriatum is however not marked in the plates on the telencephalon of the frog brain in this book. "Bei den Amphibien liegt das Stammganglion ziemlich diffus über dem Boden und der lateralen Wand, besonders die letztere verdickend, ausgebreitet." Thus, neither are any definitely defined boundaries to be found for this part, either being marked only on sagital- not on transverse-sections in the figures. In amphibians, the episphærium or pallium is bounded laterally by fovea limbica from the underlying hyposphærium, this boundary is not marked either, but should be located on the outer side below the border of the pallium. The only fovea limbica to be found on the plate is the Gaupp groove, running between lobus olfactorius and the remaining part of the hemisphere. In regard to the medial wall of the hemisphere, I beg to quote the following: "Auch sie hat bei den Amphibien so wenig Differenzierung noch erfahren, dass sie bei einzelnen Arten, ja bei Exemplaren der gleichen Art auf verschieden lange Strecken mit der ihr anliegenden anderseitigen Scheidewand, beim Frosch z. B., verkleben kann." — In order to make the topographical conditions intelligible, semi-schematic sagital-sections of various types of brain are illustrated. In regard to the amphibian brain, this section, which Edinger indicates as lying "etwas seitlich von der Medianebene", is to be found in a fully sagital position in the caudal parts of the brain, while the telencephalon is drawn in its lateral border, the whole striatum showing intersected. Septum is not mentioned in the text, but is marked on a figure of a transverse-section, on which the ventro-medial portion has been thus designated, the dorso-lateral part being termed cortex.

HERRICK (1910) divides the telencephalon of amphibians into five parts:

Bulbus olfactorius, pars dorso-lateralis, dorso-medialis, ventro-lateralis, and ventro-medialis. The boundary between the four latter parts is drawn in a horisontal direction through zonæ limitantes (HERRICK places a lateral cell-free zone immediately below regio curva). The medio-lateral limit is drawn through the ventricle in a vertical direction outwards to the surface of the brain. The dorso-lateral part is homologous with the nucleus sphæricus of reptiles and the lobus pyriformis of the higher vertebrates. The dorso-medial part he considers to be a primordium hippocampi. HERRICK discerns in pars ventro-medialis a clearly limited nucleus, which he calls nucleus medianus septi, extending both below and above foramen monroi, its dorsal part being thus homologous with KAPPERS' pars fimbrialis septi. In the anterior part of telencephalon HERRICK distinguishes a nucleus, nucleus postolfactorius (GAUPP's eminentia postolfactoria), which he considers may possibly be homologous with the tuberculum olfactorium of mammals. Moreover, in front of this nucleus HERRICK distinguishes in urodeles a medial group of cells, which he has named nucleus olfactorius anterior.

Referring to the ventro-lateral part, HERRICK says: "There is no differentiated corpus striatum in the Amphibia in the sense in which this term is used in mammals. The elements from which it is to be differentiated are present in the pars ventro-lateralis." — HERRICK derives the four caudal parts of telencephalon from the four primitive columns found in diencephalon. Pars ventro-medialis thus becomes a direct continuation of hypothalamus and so forth. The boundary groove between the pallium and subpallium, situated within regio curva (zona limitans lateralis, HERRICK), would then in diencephalon merge into sulcus diencephalicus medius. This is however a sheer impossibility, as JOHNSTON (1912) points out. Sulcus diencephalicus medius has no connection with the foramen monroi, it merges into that part of diencephalon which lies dorsal to the caudal part of telencephalon. HERRICK bases his theory on the derivation of the parts of telencephalon from diencephalon on some conditions in Ichtyomyzon, but HERRICK's construction of this brain is, according to JOHNSTON, erroneous, and thus the whole evidence for his theory falls to the ground. There is no connection between the sulci in HERRICK's figures 83 and 84. If, according to JOHNSTON, the boundary between tel- and diencephalon is laid through velum transversum and the dorsal border of the optical commissure, the diencephalic parts will project rostrally and dorsally to the hinder part of telencephalon, the grooves in the two parts of the brain running parallel and obliquely downwards from above, it is thus impossible for them to merge inte each other.

In a paper on the telencephalon in selachians (1911) JOHNSTON makes certain homological comparisons between it and the telencephalon in Rana. The boundary between the pallium and subpallium is that hitherto usually accepted. Primordium hippocampi extends also to the dorso-lateral side, but a primordum of a somatic cortex-layer may possibly be found in closest proximity to the zona limitans lateralis. JOHNSTON homologizes the lateral boundary zone (according to HERRICK) with the zona limitans lateralis of sharks, he writes: "Below the lateral zona limitans runs the lateral olfactory tract which meets with the lateral forebrain tract coming up from the thalamus. Between the two is the rounded ventral wall corresponding in position to the basal area of selachians." The lateral olfactory tract does not, however, run ventral to zona limitans lateralis (HERRICK) but dorsal to the same. In this respect JOHNSTON's account of the conditions in the frog is erroneous, as he has accepted HERRICK's boundary-zone. This boundary-zone cannot be homologized with the zona limitans lateralis of sharks, which is in fact situated above the lateral olfactory tract.

RÖTHIG (1912) was the first to give exclusive attention to the cells and their distribution in the forebrain of Amphibia. He gives in particular a very accurate and clear description of the septum and its construction. RÖTHIG is hitherto the only investigator to discern several different nuclei in the septum; thus he distinguishes between nucleus lateralis septi, nucleus medialis septi and nucleus ventro-medialis septi. Nucleus lateralis septi, situated in the caudal dorsal part of the septum, thus also forms that part of septum which KAPPERS has called pars fimbrialis septi. The medial nucleus is the continuation of a nucleus situated in the most rostral part of the ventral area of the septum; RÖHTIG calls this anterior part nucleus ventro-medialis septi. The caudal portion of the medial nucleus is further divided into a ventral and a dorsal part. In front of the septum lies a part of the telencephalon named eminentia postolfactoria by GAUPP, in contradistinction to the septum, which he calls eminentia septalis. RÖTHIG, who also describes eminentia postolfactoria, looks upon this as part of the septum, to which he also assigns the eminentia septalis and the septum nuclei. He further accepts HERRICK's division of the forebrain into five separate parts, but desires further to introduce his conception of septum as a sixth part, situated between the pars dorso-medialis and ventro-medialis. — RÖTHIG has followed the lines of the KAPPERS' school in his construcion of the pallial regions. In addition to the medial primordium hippocampi, he distinguishes a laterally situated paleocortex, which is, in its turn, divided into a lateral and a dorsal cell-plate. RÖTHIG considers that a rudiment of the epistriatum should be sought ventral to prominentia cellularis lateralis (regio curva), separated from the underlying striatum by a groove in the ventricle-wall, sulcus strio-epistriaticus. The subdivision of the lateral wall of the hemisphere in the Amphibia is in perfect agreement with the conception formulated by DE LANGE (1911). The epistriatum is assigned to the striatal parts of the telencephalon and is considered to be developed from the same; ELLIOT SMITH (1919), JOHNSTON and others, however, reject this theory, pointing out that the epistriatum (hypopallium, SMITH) is a cortical part, developed from the pallial portion of the lateral wall of the hemisphere.

RÖTHIG contests GAUPP's and HERRICK's statement that the nucleus commissuræ hippocampi is developed from the diencephalon, he considers it a continuation of the nucleus lateralis septi. It is impossible for any one who has traced the embryonic development of the amphibian brain to doubt that RÖTHIG's conception is in this case erroneous.

In his work on the septum, hippocampus and pallial commissuræ, published in 1913, JOHNSTON also treats of the frogbrain in connection with that of reptiles and mammals. He retracts in this work the homology made in his above-mentioned paper between the medial zona limitans in sharks and frogs. He now assigns the fimbrial part of the septum to the pallium; thus assigning the whole of the nucleus named by HERRICK nucleus medianus septi to the pallium, and homologizing it with the primordium hippocampi or "septum" in turtles. According to JOHNSTON's definition of the primordium hippocampi, the cell-mass, remaining after the true hippocampus-formation in the higher vertebrates has developed, is namely also a primordium hippocampi; it is this cell-mass which is known as the septum pellucidum. The hippocampal formation and septum together constitute a continuous mass of gray matter, which thickens the lamina supraneuroporica and forms the bed for the hippocampal commissure and corpus callosum. ELLIOT SMITH, who in 1903 introduced the designation primordium hippocampi in reptiles and amphibians, used it only for those parts of the reptilian and amphibian brain corresponding to the hippocampal-formation of mammals. JOHNSTON's definition thus embraces considerably more than that originally made by SMITH.

BINDEWALD (1914) has published an accurat account of the forebrain of Amblystoma, without however any fresh views on its morphology. He concurs partly in HERRICK's, and partly in RÖTHIG's conception of the Urodele brain, although disputing RÖTHIG's opinion on the existence of several septum nuclei, considering the boundaries between nucleus lateralis septi and medialis septi too indistinct to make such a division permissible in urodeles. The rudiments of epistriatum and striatum found by RÖTHIG, BINDEWALD has been unable to discover in Amblystoma. — He agrees with HERRICK in calling the medial cells which surround the rostral part of the tip of the lateral-ventricle, nucleus olfactorius anterior. This nucleus is separated laterally from the ventricular cells by a "zona limitans dorsalis" free of cells; it is more difficult to trace its boundary caudally, but BINDEWALD considers that it extends caudally to recessus caudalis (sulcus prepallialis, GAUPP).

Dorsal to the bulbus accessorius and in close proximity to zona limitans dorsalis, lies a small group of cells, called by BINDEWALD tuberculum olfactorium. Since this nucleus cannot possibly be considered homologous with that part of the brain generally known by this term, ist must be looked upon as in this case depending upon a pure mistake, tuberculum olfactorium being, as is known, a subpallial formation. — BINDEWALD has retained the old boundary drawn up by EDINGER between the telencephalon and diencephalon, which he considers more convenient although not more correct than JOHNSTON'S.

KAPPERS and HAMMER (1918) have in their description of the brain of Rana catesbyana followed the direction taken by DE LANGE and RÖTHIG, thus distinguishing both a striatum and an epistriatum, as well as a pallium divided into a primordium hippocampi and a paleopallium. In opposition to RÖTHIG, the nucleus commissurae hippocampi is assigned to diencephalon.

LUNDAHL (1918) sees in the lateral part of the pallium, i. e. in the dorsolateral part of the hemisphere, a "matrix-layer" for the remaining portion of the pallium, the medial part thus developing out of the lateral. He calls the medial part paleopallium, considering the terms archipallium or primordium hippocampi incorrect for this part of the pallium. LUNDAHL denies the existence of pyramidal cells in the amphibian brain, declaring that they appear first in reptiles, from which he draws the conclusion that amphibians, as well as other animals lacking what he calls pyramidal cells, have no cerebral cortex. The pallium of Amphibia is homologized with that of bony fishes, which according to LUNDAHL is the membraneous roof and the nucleus taeniæ situated at its fastening line. — "The brain of the Amphibia is distinguished from that of fishes chiefly by the higher development of the pallium, which is in amphibians developed into a solid, compact body, built up of nerve-cells and fibral elements." LUNDAHL goes on to say: "The dorso-medial part of the pallium of amphibians corresponds in structure to that of the paleopallium of fishes. No archipallium with its typical, simple cell-layer of pyramidal cells, nor neopallium with its pyramidal cells and cell-layer have yet formed in amphibians; the dorso-medial part of the pallium of the Amphibia must therefore constitute what I have termed the paleopallium." — Commissura pallii anterior is called commissura paleopallii. Although it is unmyelinated, LUNDAHL, who has only had Kultschitsky-preparations accessible for his investigations of the fibres, has yet described it, homologizing it with the commissura pallii anterior of fishes, which is no commissure for that part of the telencephalon, which he terms paleopallium in ganoides and teleosts. Lundahl goes on to homologize this paleopallium and its commissure with the septum pellucidum and commissura septi of amniotes. In regard to the origin and development of the various parts of the pallium, LUNDAHL concurs in JAKOB'S opinion that the paleopallium as well as the archipallium and neopallium forms in the proximity of a matrix-layer situated at the fissura marginalis; through the further development of the pallium, they become pressed over towards the medial side and down towards the septum. Thus the different parts of the cerebral cortex would originate at the same place, but be completely separate from, and develope independently of each other.

Kuhlenbeck (1921) has chiefly investigated the pallial parts of Urodela and Anura, but in connection with these, also the remaining parts of the telencephalon. He retains in the main the views of Herrick, Kappers and Röthig on the brain of the Amphibia. He endeavours to discover in this group of animals the different parts of the pallium found in the other vertebrates. He does not consider that a cerebral cortex exists, since he defines a cerebral cortex as a gray substance situated outside its fibre-tracts. Kuhlenbeck divides the pallium into three parts, a medial, a dorsal and a lateral. The two former compose an archipallium, the latter he considers to be a neopallium, all of these three parts thus constituting primordial areas of the cerebral cortices in the higher vertebrates. — The following parts are distinguished by him in the septum: Nucleus postolfactorius medialis with eminentia postolfactoria, cellulæ septales with eminentia septales, nuclus lateralis septi, pars fimbrialis septi and nucleus medialis septi. Thus, Kuhlenbeck's conception of the part termed by Gaupp, eminentia postolfactoria, is that it forms a part of the septum. He even employs the appellation eminentia septalis for this part in urodeles, although, with regard to the terminology in general use, it appears unsuitable, especially as he employs it in the same sense as Gaupp in the case of Anura. — Kuhlenbeck, however, confuses the caudal part of nucleus lateralis septi with nucleus commissuræ hippocampi, he states namely: "Das Foramen Monroi geht unter dem Septum durch, das hier zu einem kolbigen Tuberkel anschwillt und von seinen Kernen noch die Cellulæ septalis und die Pars fimbrialis Septi zeigt. Diese Zellansammlung scheint mir mit Herricks Nucleus commissuræ hippocampi, Gaupps Nucleus supracommissuralis übereinzustimmen." — Neither is nucleus medialis septi homologous with the corpus precommissurale of other writers. The ventro-lateral part Kuhlenbeck names nucleus basalis, in which he distinguishes a striatum and an epistriatum.

The granular cell-layer in lobus olfactorius is divided into two nuclei, nucleus olfactorius anterior and nucleus postolfactorius lateralis. Herrick's nucleus olfactorius anteror is however not homologous with the nucleus to which Kuhlenbeck has given this appellation, the former not being composed of granular cells. Herrick also clearly points out in his paper that the granular cells of Amblystoma do not extend medially to the anterior part of the lateral ventricle. Kuhlenbeck has in this case misunderstood Herrick's representation of the rostral part of the forebrain of urodeles. Nucleus postolfactorius lateralis appears to be only the most caudal lateral part of the granular cells. Kuhlenbeck writes of this nucleus: "Es liegt nahe, diese Gegend mit dem Lobus pyriformis der niederen Säuger zu homologisieren." It is difficult to see why this particular nucleus should be homologous to the pyriform cortex, other writers have always considered the lateral part of the pallium to be homologous with lobus pyriformis. Nucleus postolfactorius lateralis is a part of lobus olfactorius, and thus a subpallial part of the brain, but the pyriformal cortex is a pallial formation.

In a paper published in 1921 under the title of "The Connections of the Vomero-nasal Nerve, Accessory Olfactory Bulb and Amygdala in Amphibia", HERRICK describes a nucleus in the caudal part of pars ventro-lateralis and its fibre-connections, and considers that, since it appears to be connected with the accessory olfactory bulb and also has a number of fibre-connections which are characteristic of the nucleus amygdalæ of higher vertebrates, it may be homologized with the latter; he does not, however, make any decided statement on the subject; the amygdalus-complex of mammals being particularly complicated, the homology of any definite part of it with the amygdala of amphibians is very difficult.

In a paper, as yet unpublished, on the forebrain-morphology in lower vertebrates, Professor HOLMGREN makes some interesting comparisons between the inverted and everted types of brain; he points out the great conformity in the structure of these brains, in spite of the difference in their development. As the subdivisions of the forebrain of Amphibia in this dissertation is to a great extend based on Professor HOLMGREN'S subdivision of the telencephalon, it appears suitable to enumerate here the parts traced by him in the inverted brain.

I. Pallial parts:
    a) Hippocampal pallium.
    b) General pallium.
    c) Pyriform pallium.
II. Zona limitans.
III. Subpallial parts:
    d) Nucleus olfactorius and sulcus limitans lateralis.
    e) Tuberculum olfactorium.
    f) Nucleus medialis septi.
    g) Nucleus entopeduncularis, or taeniæ.
    h) Nucleus lateralis septi and, in the caudal part of the forebrain, nucleus preopticus.

A circumstance likely to prove of the greatest importance for a correct estimation of conditions in the pallium of Amphibia as well, is that Professor HOLMGREN has discovered a well differentiated cerebral cortex already in selachians. It may be noticed that this cortex is most clearly defined at the embryonic stages. Reptiles were always formerly considered to be the first in the vertebrate series of animals in which a true differentiated cerebral cortex was to be found. The occurrence of a cerebral cortex so low down in the series presents the type of brain found in Amphibia in a new light. It is possible that this brain, hitherto looked upon as embryonic, may in reality be more differentiated than has been supposed. The ventricular position of the cells may quite as well be of a secondary nature, and a migration of cells, commenced at early ontogenetic stages, have later been checked or pressed back till the cells have returned to their position near the ventricle.

In regard to the development of the various cerebral cortices in the forebrain, Professor HOLMGREN points out how erroneous is JAKOB's theory, embraced by LUNDAHL, on the origin of all these cortices in one single matrix-layer near the fissura rhinalis. "Such a matrix does not exist in the ontogenetic development. The cortices develope simply from the underlying part of the neuroblastic layer and there are no signs present of a successive displacing of cortical units from a place of origin at the "fissura rhinalis externa" to a more medial situation." The various types of cerebral cortex differentiate originally from an undifferentiated ancestral cortex, named by Professor HOLMGREN the primordial cortex.

Summary. Thus, according to current conception the telencephalon of Amphibia may be divided into a pallial and a subpallial part. The boundaries between these are drawn medially in zona limitans medialis, laterally below regio curva. (JOHNSTON's medial boundary lying more ventrally forms an exception, the septum nuclei there are assigned to the pallium.) The mediodorsal part of the pallium is indicated as an archipallium or primordium hippocampi, and its commissure as the hippocampal commissure. (LUNDAHL makes an exception in this case, calling this part paleopallium and giving its commissure a corresponding name.) The dorso-lateral part of the pallium is termed paleopallium (KAPPERS and others), neopallium (KUHLENBECK), or is considered homologous with lobus pyriformis and nucleus sphæricus (HERRICK). A striatum is located in the lateral part of the subpallium; the caudal part of the former HERRICK has separately termed nucleus amygdalæ, its dorsal part KAPPERS and others look upon as an epistriatum. Medio-ventrally lies the septum with its nuclei; according to HERRICK, BINDEWALD and others there is only one nucleus, according to RÖTHIG, two or more. The part ventral to the ventricle has occasionally been homologized with the area olfactoria of reptiles.

Pars fimbrialis septi is considered to be a subpallial formation, although not by JOHNSTON, who looks upon the whole of the septum pellucidum as being of pallial origin. ELLIOT SMITH on the contrary assigns the primordial hippocampi, which he calls the paraterminal body, likewise to the septum. All except RÖTHIG consider nucleus commissuræ hippocampi to be a diencephalic nucleus.

That part of the telencephalon lying medially between the olfactory formation and primordum hippocampi is termed eminentia postolfactoria in Anura (GAUPP and RÖTHIG), nucleus olfactorius anterior in Urodela (HERRICK), and nucleus postolfactorius medialis (KUHLENBECK). GAUPP considers it a part of the lobus olfactorius, RÖTHIG and KUHLENBECK assigning it to the septum.

Thus, although the telencephalon of Amphibia has frequently been investigated and described, we find in it certain points hitherto difficult to understand and on the signification of which opinions diverge. It is astonishing, when the fairly accessible amount of material is taken into consideration, that so extremely few investigations of the embryon have been made, and that hardly any notice has been taken of the development of the telencephalon during the larval stages, while studying its morphology. The Anura, in particular, appear to have been neglected in this respect; and it is a fact, that up to date, the embryology of the forebrain of the common frog is practically unknown. It is true, that K. v. KUPFFER (1906) gives a description of the morphogeny of the central nerve-system in HERTWIG's Handbuch der Entwicklungslehre, but it is rather scanty where it concerns the development of the telencephalon and in the description of the origin of its nuclei in Amphibia. In regard to the Anura we find a number of representations of the exterior of the brain at various stages, besides sagital sections of it at earlier stages. The description of telencephalon found there, refers to a larva at so late a stage of development that its brain structure almost corresponds with that of the fullgrown frog. The exposition of the parts of the brain is made according to GAUPP's description of the fullgrown frog, for which reason KUPFFER's account can give us no fresh views. The same is the case in regard to the urodeles, only sagital sections and plates of the exterior of the brain at early stages are given, and the text refers to these representations; the transverse sections are taken from older specimens and the description of the forebrain is exceedingly brief. In his excellent paper (1910) HERRICK illustrates and describes a number of embryons of Urodela and Anura, but these, like KUPFFER's, are only older specimens, thus the brain of a frog-embryon he shows is of an individual at a stage nearing the metamorphosis, which though appearing to be younger than that described by KUPFFER, is not sufficiently young to give any idea as to whether the structure of the telencephalon in frog-embryons resembles that in the adult animals.

Although the structure of the telencephalon in the embryons of Amphibia is little known, we often come across statements in works on these subjects declaring that the brain of the fullgrown Amphibia remains at an embryonic stage, or that it is the most embryonic of all brains in the vertebrate series. EDINGER was the first to advance this view, and he has been followed by others of the KAPPERS' school. It is the ventricular position of the cells in the telencephalon of the fullgrown Amphibia that is supposed to give it this embryonic character. For this opinion to be correct, however, it is necessary that these cells should occupy a ventricular position in the embryo, a fact of which neither EDINGER nor his followers have assured themselves.

A morphological investigation of the telencephalon, based on observation of its embryonic development, should therefore be of interest, as it would not only throw light on conditions in the forebrain of the larva of Amphibia, but also on some of those in the fullgrown Amphibia, which have hitherto been confused. Thus the question as to where the boundary between the pallial and subpallial parts should be drawn is not yet satisfactorily solved. Although all investigators have drawn the lateral boundary ventral to regio curva, weighty reasons are to be found against placing it so far down towards the ventral side. The lateral olfactory tract of Amphibia would, namely in that case, lie dorsal to this boundary zone in an area assigned to the pallium. The characteristic position of the olfactory tract of other lower vertebrates is ventral to zona limitans lateralis outside a subpallial nucleus, nucleus olfactorius lateralis. Medially it is the fimbria and their relation to the septum and the hippocampal formation, which have not yet been decisively investigated in Amphibia. JOHNSTON's and ELLIOT SMITH's views are on this point diametrically opposed to each other. Such a fundamental question as the limitation of the pallium in the direction of the subpallium, does not either appear to be definitely answered, and yet on it depends practically the whole of the comparative anatomy of the amphibian brain. It is naturally impossible to undertake any really detailed comparison between the brain of the Amphibia and that of other lower as well as higher vertebrates, until this boundary has been determined. The terms striatum and epistriatum as well as septum and primordium hippocampi in Amphibia are mere empty words without this boundary, these parts receiving their chief characteristic from their position in relation to the said boundary.

I will therefore, in the following investigation, attempt to determine the boundary between the pallium and the subpallium, starting from the ontogenetic development of the amphibian brain, and draw the conclusions which necessarily follow.

MATERIAL AND METHODS.

The material used for the investigation of the brain of Anura consisted of about a hundred series of sections of Rana, of which some have been impregnated according to CAJAL's, BIELCHOWSKY's and GOLGI's silver methods, some stained according to WEIGERT's hæmatoxylin method for myelinated fibres, and some with chresylviolet for staining the cells. Frog-embryons have been fixed for investigation in CARNOY's or BOUIN's fixation fluids. Larva have been measured after fixation and preservation in 90 % alcohol. Series of frontal, sagital and horizontal sections have been made, stained with hæmalum, chresylviolet or F. C. C. HANSEN's hæmatoxylin. — Besides Rana, various series of Bufo, Pipa and Pelobates have been investigated; these series consisted partly of adult specimens, partly of larva.

Complete series of sections have been made of the brain in urodeles of the families of Salamandra, Triton and Amblystoma, of adult specimens as well as at the larval stage. Triton embryons have been treated in the same manner as those of frogs, and have also been measured after fixation. Fibre preparations have likewise been employed of Triton and Salamandra.

Series of sections of cyclostomes, sharks, bony fishes and reptiles have been used as comparative material, as well as a series of Protopterus and of reptile-embryons and birds. All these series belong to the Zootomical Institute's collection of neurologic preparations, kindly placed at my disposal by Professor NILS HOLMGREN, to whom I owe a great debt of gratitude for this advantage and for the interest he has always shown in my work, as well as for the advice and hints he has given me.

DESCRIPTION OF THE TELENCEPHALON IN FROG-EMBRYONS.

Length: 0,8 cm. — The telencephalon is at this stage vesicular. Its sides, "lateral plates", are much thickened. In front of the commissural-bed, already clearly defined, these lateral plates are connected along their whole border, thus ventrally as well as rostrally and dorsally, by a continuous epithelial membrane, representing the anterior part of lamina terminalis, the entire lamina supraneuroporica and the tela of the forebrain.[1] The edges of the lateral plates lie close together ventrally; dorsally and rostrally they are further apart, thus causing the dorsal and rostral part of the connecting membrane to become wider than the ventral.

In front and above, the lateral plates show a tendency to form the future hemispheres, their rostral and dorsal edges being curved inwards towards the medial line. The anterior curve has resulted in the anterior epithelial membrane becoming concave to the brain ventricle in the form of a shallow fold (Fig. 1, *f. t.*). In the dorsal tela, which forms a direct continuation of the anterior connecting membrane, a faint continuation of the above-mentioned fold is visible.

On the lateral side of the vesicular rudiment of the telencephalon, considerably caudal to its anterior edge, lies the rudiment of bulbus olfactorius (fig. 1, *bulb. olf.*). Its position is slightly ventral to the dorso-ventral central line of the telencephalon, not fully ventral as at later stages (fig. 2, *bulb. olf.*).

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[1] As the location of the recessus neuroporicus cannot be practically determined in amphibians, I have preferred not to use the terms lamina supraneuroporica and terminalis for this epithelial membran.

The lateral plates are completely filled with cells, which are very densely packed, especially in the neighbourhood of the ventricle. Dorso-laterally, towards the surface of the brain, the density of the cells appears to diminish. A well-defined differentiation is visible in this cell-mass close to the rudiment of the bulbus, where a long, narrow cell-free segment is to be found, extending along the surface of the brain vesicle, over the entire middle third part of the latter.

On the transverse section the ventricle is pear shaped in all its parts, whith the thicker end pointing upwards (fig. 2). It is only furthest frontad on the very earliest transverse sections of the series that it shows ∞-shaped through the inward curving of the rostral edges of the lateral plates, i. e. through the beginning septum formation.

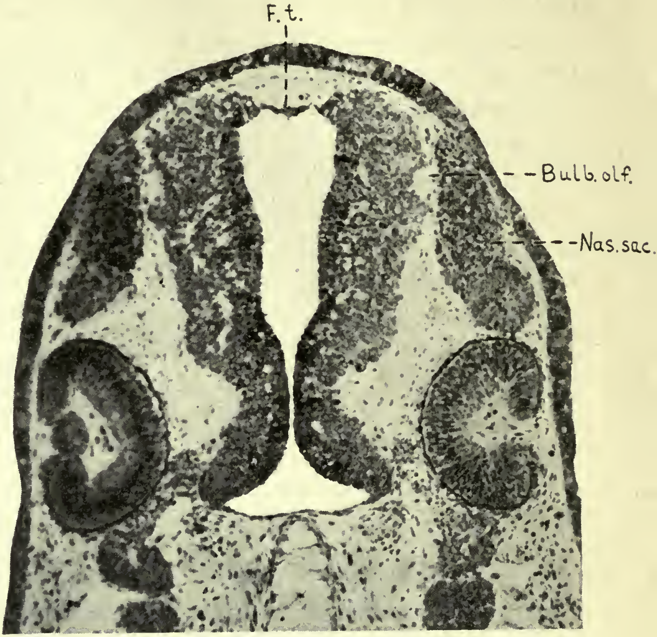

Fig. 1. Rana, 0,8 cm. Horizontal section. *Bulb. olf.*, bulbus olfactorius. *F. t.*, forebrain tela. *Nas. sac.*, nasal sac.

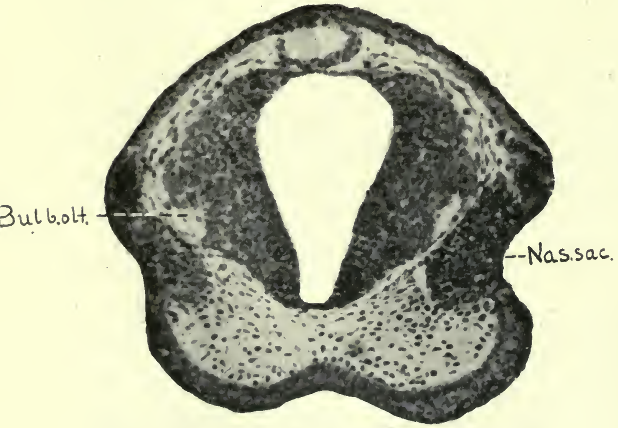

Fig. 2. Rana, 0,8 cm. Cross section *Bulb. olf.*, bulbus olfactorius. *Nas. sac.*, nasal sac.

No defined grooves are visible on the ventricular surfaces of the lateral plates, but the inward curving of their dorsal edges seems to indicate the spot where, at a later stage, a distinct ventricular groove will appear.

Length: 0,9 cm. — The lateral plates in the telencephalon have become thickened and the dorsal inward curving has continued, causing the brain vesicle to become lower than before and relatively broader (fig. 5). Rostrally the lateral plates have increased in size, becoming still more concave towards the medial line. Thus the formation of the hemisphere has proceeded.

On the outer dorsal surface of the lateral plates a longitudinal groove *E* has appeared (figs. 3, 5, *E*), dividing this surface into a medial and a lateral part. The groove does not originate at the rostral edge, but some distance beyond it. On the series of transverse sections it is first visible on the sections lying behind the rudiment of bulbus olfactorius, after which it can be traced caudad through some ten sections. The groove is particularly deep and well-defined; it extends to the ventricular cell-layer, thus separating a dorsomedial outer cell-area from the remaining part of the telencephalon's outer cell-layer. Where groove *E* stops, viz. caudally to it, an incision in the dorsal edge may be noticed on some of the sections, which bears a striking resemblance to the image of the groove itself on the transverse sections, these occasional incisions having the same position as the groove, and also extending toward the ventricular cell-layer. These incisions are evidently caused by blood-vessels, which one by one force their way into the brain just beyond this line.

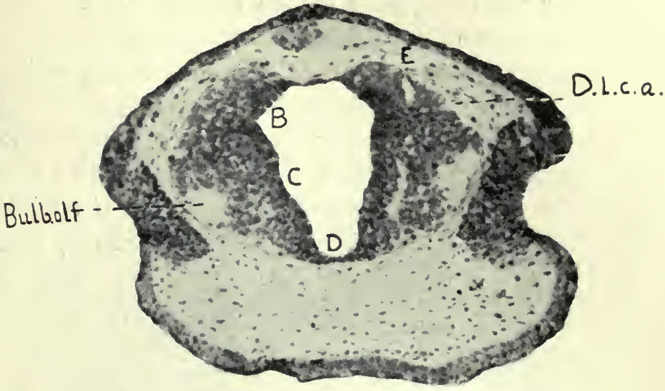

Fig. 3. Rana, 0,9 cm. Cross section through the middle part of the forebrain. *Bulb. olf.*, bulbus olfactorius. *D. l. c. a.*, dorso-lateral cellfree area.

Bulbus olfactorius has retained its position on the lateral side (figs. 3, 4, *bulb. olf.*), although lying somewhat more ventrally, and also extending further rostrally than was previously the case. Nervus olfactorius enters the brain at right angles from the side. — In the commissural-bed commissura anterior is visible, a trace of which is already found at the 0,8 cm. stage; it runs beside the ventral surface immediately in front of the preoptic recess, separating the cells found there from the ventral surface of the brain.

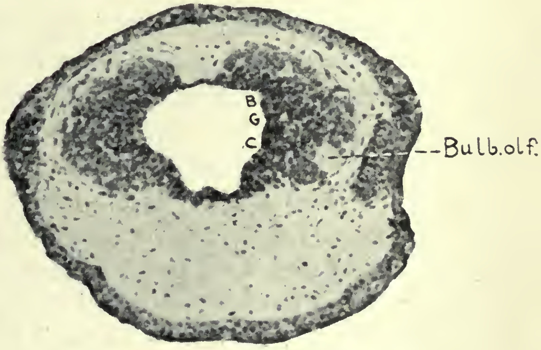

Fig. 4. Rana, 0,9 cm. Cross section through the rostral part of the forebrain. *Bulb. olf.*, bulbus olfactorius.

The ventricular surface of the lateral plates is grooved (figs. 3, 4). The most dorsal of the grooves, *B*, is that indicated at a previous stage as originating through the incurving of the dorsal edges of the lateral plates. Groove *B* extends from the most rostral part of the ventricle at the anterior epithelial membrane through the entire telencephalon. Caudally it droops downwards, the rostral part of the diencephalon at the same time overhanging the posterior parts of the telencephalon. In the central part of the telencephalon (fig. 5) the outer groove *E* lies opposite the inner groove *B*, where the medio-dorsal part is thus bounded on both the outer and inner sides.

Ventral to groove *B* runs groove *C* (fig. 3), which also commences at the anterior edge, it runs ventro- caudally through the rostral part of telencephalon and unites with the medial floor groove *D* at the anterior edge of the commissural-bed. Between *B* and *C* an insignificant groove *G* (fig. 4) is visible furthest frontad, traceable for only a short distance caudad, it being as yet impossible to determine where it ends.

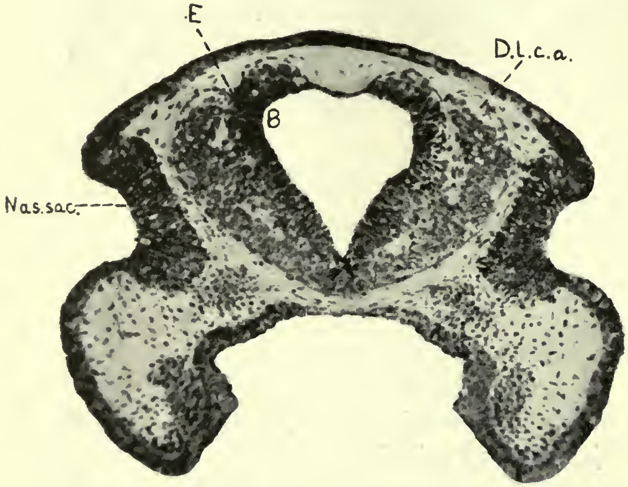

Fig. 5. Rana, 0,9 cm. Cross section through the caudal part of the forebrain. *D. l. c. a.*, dorso-lateral cellfree area. *Nas. sac.*, nasal sac.

The lateral plates are still completely filled with cells, with the exception of a small area situated at the dorsal surface (fig. 3, *D. l. c. a.*), and the partly cell-free rudiment of the bulbus. Round the ventricle the cells are very closely packed, are elongated and have their longitudinal axes directed towards the ventricle. Towards the periphery the cells are considerably more diffuse and are round in form. Thus it is easy to distinguish between an inner ventricular and an outer cell-layer; the two cell-layers are frequently separated from each other by narrow fissurelike formations, devoid of cells (fig. 3). — The above-mentioned dorsal cell-free area, identical with that described at the 0,8 cm. stage, commences dorsally to the bulbus olfactorius and extends caudally to the region of the commissura anterior, where it becomes united with the cell-free parts connected with the commissures. This cell-free part is situated laterally, and in close proximity to the outer groove *E*, and is probably composed of olfactory fibres.

Length: 1,0 cm. — Through continued evagination the two lateral plates have become curved outwards in front of the medial epithelial membrane, which was originally the terminal part of the telencephalon. In consequence of this, the previously rostral parts of the lateral plates take up a position caudal to the anterior edge of the brain, as though curved inwards and caudad along the medial line. The inversion has also continued, the dorsal edges of the lateral plates becoming curved much deeper downwards. The ventral floor parts have undergone great thickening while at the same time nearing one another. — The direct consequence of the evagination and inversion is the formation of two small lateral ventricles, separated from one another by the newly formed parts of the septum (fig. 6). The rostral epithelial membrane is connected with the posterior edge of the septum; the fold in this membrane has become more clearly defined by these in-curved lateral plates being closely pressed against each other. Beside the connections of the membrane runs a fairly deep groove in a ventro-dorsal direction, causing the fold to appear like a wedge between the two parts of the septum, visible on transverse sections already rostrally to foramen monroi, projecting downwards between the medial walls of the hemispheres. At foramen monroi, this epithelial fold is seen on the transverse sections still lying between the lateral ventricles. Dorsally the epithelial membrane continues as before in the epithelial tela, which becomes connected with the medial edge of the pallium a little higher up. The fold in the dorsal membrane can be traced towards that part of the telencephalon lying directly dorsal to the commissural-bed.

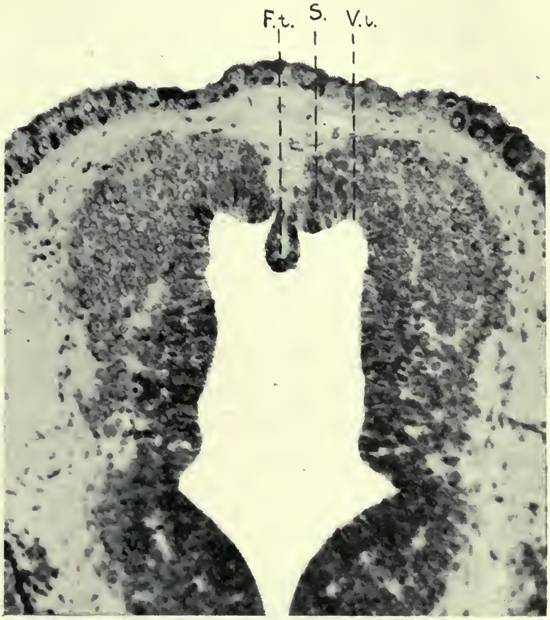

Fig. 6. Rana, 1,0 cm. Horizontal section. *F. t.*, forebrain tela. *S.*, septum. *V. l.*, lateral ventricle.

The longitudinal groove *E* may still be found on the outer surface of the lateral plates.

Bulbi olfactori extend along the ventro-lateral surface of the hemispheres Their anterior parts extend, as a result of evagination, almost to the rostral edge of the brain. The junction of the olfactory nerve is found nearly on a level with foramen monroi.

The lateral ventricles are rather shallow, projecting only halfway into the evaginated area in front of foramen monroi (fig. 6). In cross-section they are elliptical in shape, having their longitudinal axe in an almost horizontal position; their outer part lying, however, somewhat more ventrally than the medial. At foramen monroi and in front of the commissural-bed, the two lateral ventricles become united with the floor of the medial ventricle; the latter remaining in the shape of a small pouch on the sagital plane between the caudal part of the septum and the rostral edge of the commissural-bed.

The grooves in the ventricular surfaces are those familiar from the preceding stage. They are indistinguishable within the lateral ventricles, but visible behind foramen monroi. The curving process of the roof-section has continued. Groove *B* is at this stage only visible as a powerful curve within the medial ventricle. Through the commissural-bed runs a solitary medial groove, *D*, being a continuation of the narrow ventricular pouch situated in front of the commissural-bed. In recessus preopticus a groove may be distinguished running from the rostro-dorsal part to the caudal ventral corner, a groove which is still found in the adult frog.

Length: 1,1 cm. — At this stage the two hemispheres are fairly well-developed, with lateral ventricles, extending considerably further frontad towards the rostral edge of the brain than previously. The ventral parts of the hemispheres have become connected with each other a little before foramen monroi, but only for a short distance; the united part is situated close to the ventral border. Higher up the hemispheres are divided by the epithelial fold. The outer groove *E* may here be found again in the evaginated part of the telencephalon, thus running on the outer dorsal wall of the hemisphere.

Bulbus olfactorius increases constantly in size, its cell-free part lying as before, ventro-laterally along the entire hemisphere (fig. 7). Caudally we may see this cell-free area, which is composed of glomeruli olfactorii, divided into two parts by immigrated ganglion cells. The area thus detached, is situated in the dorso-caudal part of the bulbus; it is this area which is the rudiment of bulbus olfactorius accessorius, which thus is originally only a part of the primary laterally situated olfactory bulb (fig. 7, *Bulb. acc.*).

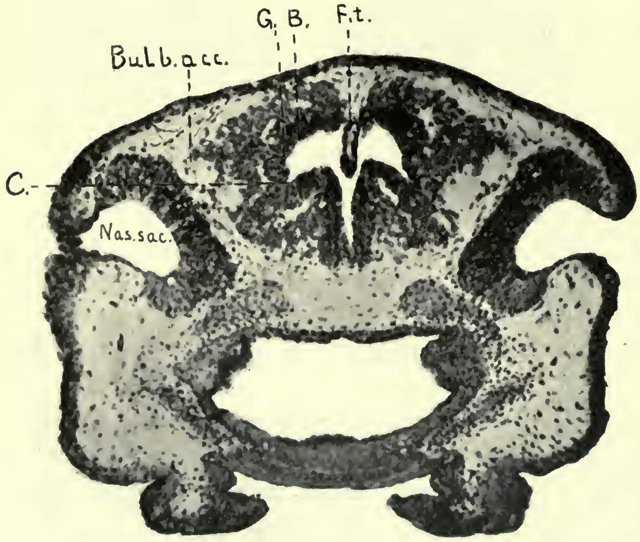

Fig. 7. Rana, 1,1 cm. Cross section on a level with the foramen monroi. *Bulb. acc.*, bulbus accessorius. *F. t.*, forebrain tela. *Nas. sac.*, nasal sac.

The most remarkable fact which comes to light during investigation of the different series of transverse sections of frog-embryons of 1,1 cm. length, is the varying shape of the lateral ventricles. Some, as at stage 1,0 cm., are elongated horizontally, very low, but rather broad, some, on the other hand, are more open and wide, with numerous grooves, and extending obliquely with the lower pointed part in a ventro-lateral direction (fig. 7). In the latter case the most rostral part of the lateral ventricle appears as a nearly vertical fissure, further caudad it widens upwards, while the pointed ventral part extends more laterally.

The longitudinal ventricular grooves extend into the lateral ventricles, they are especially well-defined when the latter are of the open type. The ventral groove *C* may there be traced from the rostral edge of the lateral ventricle right up to the rostral edge of the commissural-bed, where it descends into the above-mentioned central groove *D*. Groove *B* also seems to originate as far forward as possible in the lateral ventricle, of which it forms the lateral corner. It may be traced past foramen monroi, but disappears immediately behind the same, the entire lateral ventricular wall here bulging outwards.

A groove is also to be found on the surface of the medial ventricle, this is sulcus limitans internus, which forms the boundary between the pallial and subpallial parts of the septum. This groove extends through the whole of the lateral ventricle, from its most rostral part to foramen monroi, where it ends dorsally at the upper epithelial membrane.

Between grooves *B* and *C* we find yet another groove, *G*, in the neighbourhood of foramen monroi or behind the same. It begins at *C* and runs obliquely caudad and upward to fuse with *B* in the more caudal part of the telencephalon, thus dividing the part *B*—*C* into two parts, a dorsal and a ventral (fig. 8).

The ventricular grooves are as above-mentioned less well developed in the type of forebrain in which the lateral ventricles are horizontally-placed narrow fissures. The lateral corner of the ventricle corresponds there with groove *B*. Groove *C* is developed in those cases where the ventricle extends medially somewhat downwards along the central line. Medially sulcus limitans internus is well developed; the groove *G* is indistinct in these brains.

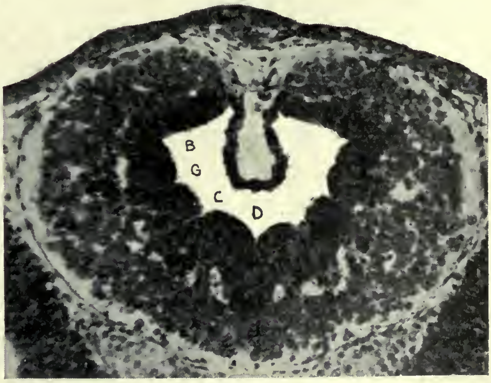

Fig. 8. Rana, 1,1 cm. Cross section through the hind part of the telencephalon.

Within the hemispheres the lateral parts are the most developed. The septum is a narrow part as yet quite insignificant. It continues caudad in the epithelial membrane which at earlier stages represents the lamina terminalis and supraneuroporica. — The only cell-free areas in the hemispheres are the glomeruli part of the bulbus and the dorso-lateral area, situated at groove *E*, mentioned at the 0,9 cm. stage, and in the hind part of telencephalon that part of the commissural-bed where the commissura anterior passes, viz. the lateral and ventral parts.

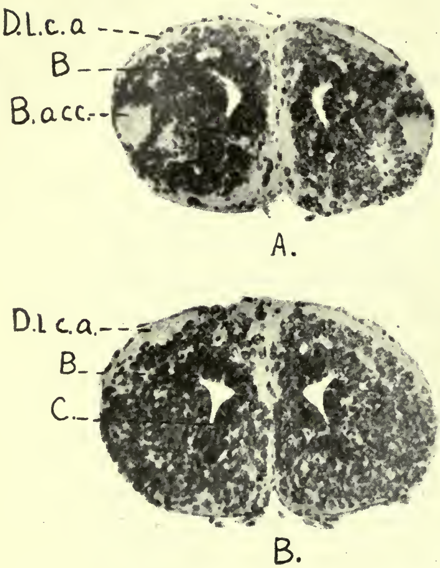

Fig. 9. Rana, 1,2 cm. A. Cross section through the rostral part of the forebrain. B. Cross section from the same series further caudad. *B. acc.*, bulbus accessorius. *D. l. c. a.*, dorsolateral cellfree area.

Length: 1,2 cm. — The two hemispheres appear distinctly in the dissected brain. Bulbi olfactorii are situated at the anterior edge of the brain, extending caudad for a short distance along the lateral edge, but do not reach even halfway towards foramen monroi. The accessory bulbs have become still further removed from the primary olfactory bulbs by the immigration of ganglion cells, and are visible on the transverse sections as small cell-free parts on the first section on which the lateral ventricle was found (fig. 9a, *bulb. acc.*). Nervus olfactorius enters the anterior edge of the hemisphere ventro-laterally.

The fusion of the ventral parts of the hemispheres at foramen monroi has continued. At the same time the medial ventricular pouch, which extended between the commissural-bed and the "rostral epithelial membrane" has disappeared, so that the ventral part of the evaginated brain has become fused with the commissural-bed. Of the ventricular pouch only a medial groove *D* remains, forming a rostral continuation of the groove running medially through the commissural-bed.

The fold in the epithelial membrane remains, as well as its dorsal continuation extending far down in the medial ventricle (fig. 10). — Groove *E* is to be found in the dorsal outer wall of most of the brains dissected at this stage, lying on a level with or behind foramen monroi, but is exceedingly short and seems on the point of vanishing.

As at the 1,1 cm. stage, the lateral ventricles are of varying shapes, in some of these brains the horizontally-placed fissurelike ventricle remains, others have lateral ventricles which by their shape constitute a transition of the form of the ventricle partly in the preceding, partly in the succeeding stages. The brain here illustrated is that which is most typical for the 1,2 cm. stage. The lateral ventricles, as shown in the figure, resemble the wide-shaped ones described at the preceding stage. Grooves *B* and *C* are sharper than before (fig. 10). Sulcus limitans internus forms caudally the dorsomedial corner of the ventricle, it droops downward further frontad till it lies in the centre of the medial wall (fig. 9b, 10, *A*). At foramen monroi a sharp ventro-medial groove is visible in the wall of the lateral ventricle, this is the solitary medial groove *D*, which at the "rostral epithelial fold" divides into the two grooves forming the boundary of this fold and running along the caudal edge of the septum.

The ventricular and the outer cell-layers are distinctly separated from each other. The outer cell-layer no longer extends to the outer surface of the hemisphere, with the exception of a cell-mass laterally close behind the bulbus olfactorius, and of a few solitary cells in the dorso-medial part which also extend to the surface.

Length: 1,3 cm. — The two hemispheres have become considerably enlarged in consequence of continued evagination; the greater part of telencephalon has become involved in the process of evagination. Bulbus olfactorius is a powerfully developed part, having now reached its final position in the ventro-rostral part of the hemisphere. The bulbus parts of the two sides are for the present completely distinct from each other; the glomeruli do not extend to the medial edge, being separated from the latter by a narrow layer of ganglion cells. — On the outer dorsal surface of the hemisphere we find a last trace of groove *E*, in a corresponding position to that of the 1,2 cm. stage, i. e. in the neighbourhood of foramen monroi; at the succeeding stages this groove has completely disappeared.

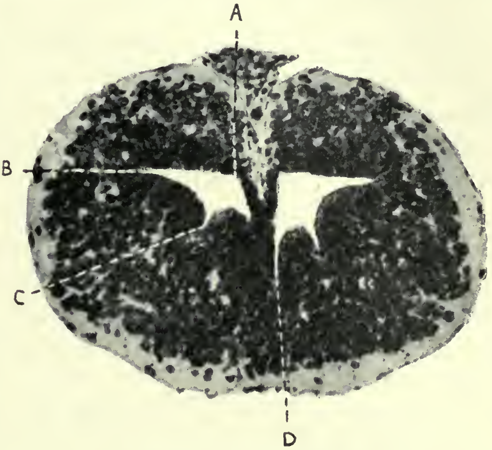

Fig. 10. Rana, 1,2 cm. Cross section close to the foramen monroi (the same series as the last).

The lateral ventricles have again taken a different shape. The sharp grooves with the convex parts between them have become reduced. The ventricles have become wider and more rounded in form. The grooves are yet visible, although only forming shallow concavities in the wall of the hemisphere. The most distinct is the medial sulcus limitans internus, which together with grooves *B* and *C* gives the central part of the lateral ventricle the form of a triangle.

A dorsally situated, smaller commissure is now visible in the commissural-bed, in addition to the wide ventral commissura anterior. This is commissura pallii anterior, which runs between the ventricular and the outer cell-layer in close proximity to the ventral surface of the ventricle. It runs caudal to commissura anterior at the posterior edge of the commissural-bed, between the caudal parts of the pallium. Dorsal to the commissura pallii anterior, the outer pallial cells have disappeared, and close to the ventricle a cell-mass protrudes dorsally from diencephalon, this is nucleus supracommissuralis (Gaupp).

The cells in the periphery of the hemisphere are now no longer so closely packed. The dorso-lateral cell-free parts have at the same time become larger. The septum part has increased more than the lateral parts of the hemisphere, making it comparatively thicker than before. The lateral parts are as yet, however, the most powerfully developed, the ventro-lateral walls surrounding the lateral ventricle furthest frontad are in particular very thick. Behind bulbus olfactorius the ventro-lateral cell-layer is very closely packed, these cells extending here to the other surface. Further caudad the cells become less dense, and on the medial side they separate from the outer wall. A part of the dense ventral cell-layer behind the bulbus is now seen stretching up in a dorsal direction through the subpallial part of the septum. This is the first rudiment of nucleus medialis septi, which originates from the ventral cell-mass that forms the most caudal part of the bulbus, i. e. its granular cell-layer.

The ventricular cell-layer which at earlier stages has been nearly as powerful as the outer, is at this stage far less dense. It is least powerful in the dorso-medial walls of the hemispheres, dorsal to sulcus limitans internus. Here the outer cells almost reach the ventricle. Opposite the groove, the pallial and subpallial cells become somewhat separated in the outer layer, forming a primary rudiment for the medial cell-free boundary in the septum, zona limitans medialis. The disposition of the outer cells in the dorso-medial part differs from that in the remainder of the hemisphere, in the former case they are disposed more uniformally, while in the other part they appear as if migrating in flocks from the ventricular layer. The cells in the pallial part are larger than those in the other parts of the telencephalon, the outermost are elliptic in form, extending in the direction of the surface of the brain.

The reduction of the rostral sagital ventricular pouch is completed. The groove of which a trace yet remained at the preceding stage, has disappeared, as well as the medial groove *D* in the commissural-bed. The fold in the rostral epithelial membrane has at the same time become reduced. The image of the foramen monroi on the transverse section is therefore quite a new one. The dorsal epithelial fold is small in the immediate proximity of foramen monroi, further caudad it disappears entirely, to increase again in size in the most caudal part of the telencephalon, there to become the origin of plexus chorioideus which extends deep down into the medial ventricle.

Length: 1,4 cm. — This is the earliest stage at which the two bulbi olfactori are connected with each other, a small bridge having formed between the bulbi in the centre of the glomeruli layer. This bridge is situated at the dorsal edge of the glomeruli, close to the mitral cell-layer lying above it.

The ventricles in the hemispheres are of the same type as at the 1,3 cm. stage, although somewhat rounder and wider. Sulcus limitans internus is clearly visible through the entire length of the ventricle. The grooves *B* and *C* are distinct at intervals, *C* being most clearly defined in the rostral parts, *B* in the proximity of foramen monroi, partly within the lateral ventricle, partly in ventriculus impar.

The septum and the dorso-medial part have become thickened. The walls of the hemispheres are of an even thickness, proving that development has been more vigorous in the medial and dorsal than in the ventral and lateral parts. The cells are forced more and more from the surface of the brain by newly-formed fibre-connections; where they still extend to the surface, as is the case in the pallium, they are very sparse. Nucleus medialis septi has increased in size, extending further both caudally and dorsally than before. Ventral to sulcus limitans internus, immediately before foramen monroi, a nucleus begins to differentiate from the ventricular cell-layer, this is nucleus lateralis septi, that part of the septum which in the adult frog forms the so-called fimbriate nucleus.

Length: 1,5 cm. — The process of fusion between the two glomeruli parts of the olfactory bulbs has become more comprehensive. The bulbs form at this stage a powerful part stretching far in front of the rostral parts of the lateral ventricles. The glomeruli lie ventrally, and it is only furthest forward that they embrace the dorsal surface as well. They extend obliquely downwards and caudad, and attain with their most caudal part the glomeruli portion of the accessory bulbs, below the rostral edge of the lateral ventricles. The accessory bulbs are still closely connected with the rostral bulbs; they consist of a spherical aggregation of glomeruli separated from the glomeruli layer of the anterior bulbs only by a layer of ganglion cells.

The evaginated part of the telencephalon has increased in size with immense rapidity. The bulk of the lateral ventricles is increased by evagination, the walls become thinner from the continued extension, and the cells, not having multiplied in proportion to the growth of the brain, lie scattered more and more sparsely (fig. 11). As above-mentioned, the growth of the hemispheres is not uniform, it is far more vigorous medially than laterally, which is evident from the increasing thickness of the medial wall, while the lateral wall becomes relatively thinner. During this time, while the cells become more and more separated from each other, and from the outer wall, the increase of matter in the forebrain takes place mainly by the increase of neurites and dendrites.

The cells lie more sparsely scattered in the dorso-medial part of the hemispheres (fig. 11). The ventricular cell-layer here is thin, consisting only of one or two rows of longitudinal cells. In immediate proximity of the ventricular cells the large round peripherial cells are to be found; they are most densely packed towards the ventricle; this cell-layer becomes continually more sparsely scattered towards the periphery. Laterally the ventricular cells increase in number. The emigrating cells do not here attain the surface; they lie in a closely packed mass, separated from the inner layer of cells by fissure-like formations. Ventrally the ventricular layer increases still more, the density of the outer layer here also becoming greater. The size of the cells in this peripheral layer diminishes, however, somewhat down towards the ventral side. In the subpallial part of the septum the ventricular cell-layer attains its greatest density; while dorsally to sulcus limitans internus it consists only of a single layer, it is here a dense cell-mass with at time a five- or six-fold layer of cells. These ventricular cells are rounder in form than the others, which stretch towards the ventricle. The cells in the caudal subpallial part of the septum extend as far as the outer edge. The two septal nuclei are here in process of development, the medial one, forcing itself from the front caudad and upward along the medial surface, and the lateral, which developes along the ventricular wall and pushes forward medially, in the contrary direction therefore to nucleus medialis septi.

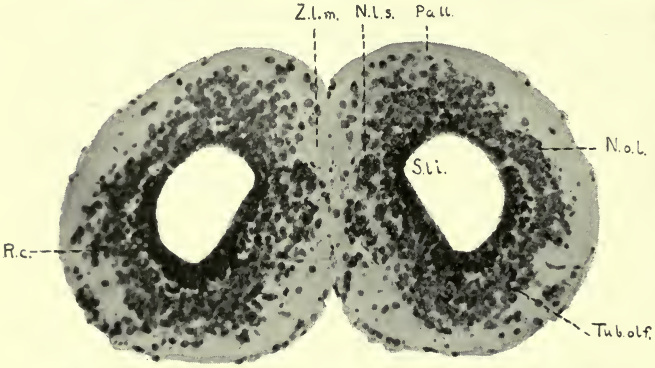

Fig. 11. Rana, 1,5 cm. Cross section. *N. l. s.*, nucleus lateralis septi. *N. o. l.*, nucleus olfactorius lateralis *Pall.*, pallium. *R. c.*, regio curva. *S. l. i.*, sulcus limitans internus. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

Of the ventricular grooves, we find sulcus limitans internus, the ventral groove *C*, and laterally a groove which seems to be that described at earlier stages as *G*, which ran between grooves *B* and *C*, dividing the area between the latter into two parts. In the outer cell-layer beyond groove *G*, a cell-free incision is visible, laterally to which the peripheral cells run down in a wedge in the direction of the ventral surface (fig. 11, *R. c.*). This projecting part of the ventro-lateral cells originates behind the accessory bulbs, where the granular cells first extend as far as the outer edge; above these granular cells, are disposed some of the peripheral cells of the lateral part; when, further caudally, the granular cells disappear, this upper cell-wedge remains. This convex tongue-shaped cell-wedge stretches through the entire hemisphere as far as foramen monroi.

Length: 1,8 cm. and 2,0 cm. — No important alteration takes place in the telencephalon at these stages. Development proceeds along the same lines as in the preceding stages. The fusion of the two bulbi continues, till it finally extends in a caudal direction on a level with the rostral edge of the lateral ventricles and likewise embraces the ventral glomeruli part which was not hitherto connected with it.

The ventriculus impar has become very broad, like the lateral ventricles, it is large and wide. The floor of the medial ventricle juts upwards medially in the form of a ridge towards the same, on the same spot at which in younger embryons a groove down to the commissural-bed was found.

Length: 2,5 cm. (hindlegs: 0,5 mm.). — The lateral ventricles have become extended in a dorso-ventral direction along the greater part of the hemispheres. It is only furthest dorsally and caudally that they extend in a more horizontal direction. Simultaneously with the disappearance of the rounded form, a number of the old ventricular grooves have again become visible. The dorsal part of the ventricles is round, the ventral part is on the contrary pointed. This pointed part corresponds with the floor groove *C*, which has never entirely vanished. Groove *G*, shallow, but quite distinct, runs in the lateral walls inside the projecting cell section described at an earlier stage (fig. 11, *R. c.*). Dorsal to *G*, groove *B* again becomes visible, running ventral to the dorsal edge of the ventricle in the central part of telencephalon. Further caudad at foramen monroi, groove *B* rises towards the dorso-lateral corner of the ventricle. In the medial wall, sulcus limitans internus is clearly visible through the entire ventricle. In the caudal part of the hemisphere, zona limitans medialis extends up to the ventricle, thus dividing all the peripheral cells in the caudal edge of the septum into two parts: a pallial and a subpallial.

A number of complications have arisen at the foramen monroi in consequence of the vigorous development of the septum nuclei, nucleus lateralis septi having been forced caudad and upward along the medial edge during its growth, the caudal part of zona limitans medialis becoming thereby almost vertical in position. At foramen monroi this septum nucleus now becomes visible forcing itself up dorsally to foramen, pushing zona limitans before it (fig. 12). Thus, in the upper medial corner of each half of the telencephalon a small nucleus lies dorsal to foramen monroi, separated from the pallial parts by a cell-free boundary. This is the first rudiment of partes fimbrialis septi, and is consequently formed of subpallial parts, which by their vigorous growth have been forced past and dorsal to foramen monroi. In consequence of the appearance of these fimbrial parts, the caudal part of sulcus limitans internus runs in that portion of the medial wall situated dorsally to foramen monroi; from the inner wall of the lateral ventricle it goes out later into the upper part of the medial ventricle. It has its terminal point, however, at the same spot as before, viz. beside the dorsal epithelial fold, which is connected with the medial edge of the pallium.

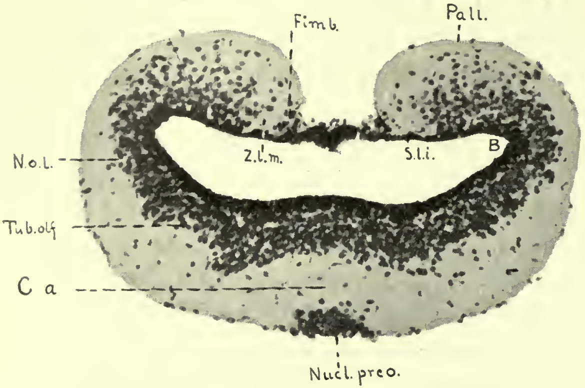

Fig. 12. Rana, 2,5 cm. Cross section behind the foramen monroi. *C. a.*, commissura anterior. *Fimb.*, fimbria. *N. o l.*, nucleus olfactorius lateralis. *Nucl. preo.*, nucleus preopticus. *Pall.*, pallium. S. l. i., sulcus limitans internus. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

As above-mentioned, the lateral nucleus has powerfully increased, not only in a caudal direction, but extending also further rostrally than before. Its cells have become separated from the ventricular cell-layer in small groups or rows, which approach the medial edge. — The medial septum nucleus is of less importance, it is situated in the rostral part of the brain along the medial wall, in front of the region over which the lateral nucleus extends.

Laterally and ventrally a powerful cell-free layer surrounds the outer walls of the hemispheres. The peripheral cell-layer has, especially in the lateral wall, become much less thick; the ventricular cell-layer there has also diminished. It is only in the subpallial part of the septum that a denser ventricular layer of cells remains, clearly consequent upon the continued vigorous development of this part of the brain. Dorso-medially the outer cells are disposed in rows in the direction of the ventricle, more densely packed near the latter and more sparsely towards the periphery as at the preceding stages.

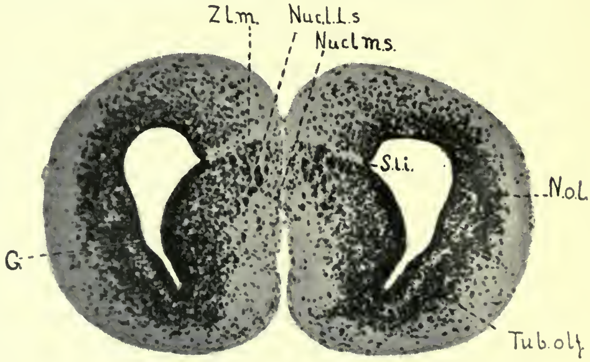

Fig. 13. Rana, 3,5 cm. Cross section. *Nucl. l. s.*, nucleus lateralis septi. *Nucl. m. s.*, nucleus medialis septi. *N. o. l.*, nucleus olfactorius lateralis *S. l. i.*, sulcus limitans internus. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

Length: 2,8 cm. (hindlegs: 2 mm.) and 3,0 cm. (hindlegs: 3 mm.). — As these two stages correspond fairly well with the previous one and no particular fresh developments in growth are to be noticed, I will pass on to the following stages.

Length: 3,2 cm. (hindlegs: 4,5 mm.) and 3,5 cm. (hindlegs: 6 mm.). — At the earlier of these two stages, the lateral ventricles show a tendency to stretch in a dorso-lateral direction, which is completed at the later stage (fig. 13). The ventricles only become round frontad towards the formatio bulbaris. They are still widest dorsally, while the ventral part is almost fissurelike in places. Their form is singularly irregular, the walls of the hemispheres curving inwards towards the ventricle both medially and laterally. At the foramen monroi the ventricles are still rather wide; they now project into the caudal part of the hemisphere, thus, in consequence of continued evagination, the posterior horn of the ventricle have developed; the hemispheres also being evaginated in a caudal direction (fig. 14).

The ventricular grooves are: sulcus limitans internus, the ventral groove *C* and the lateral grooves *B* and *G*. Sulcus limitans internus is indistinct in the rostral part of the ventricle; when first visible on the transverse section it is situated approximately in the centre of the medial wall. Further caudad it rises upwards, at the same time becoming deeper. Passing foramen monroi, it becomes a groove in the medial ventricle and ends as before at the dorsal epithelial membrane. Groove *B* is only visible at the earlier of the two stages. Groove *G* is on the contrary most distinct at the later stage. Here the lateral wall of the hemisphere forms two ridges in the direction of the ventricle, between which groove *G* runs in a fairly ventral direction (fig. 13).

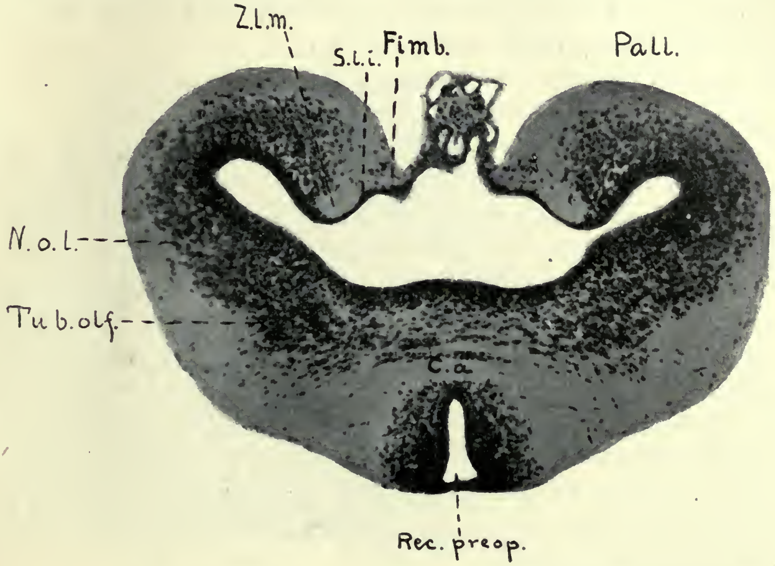

Fig. 14. Rana, 3,5 cm. Cross section behind the foramen monroi. *C. a.*, commissura anterior. *Fimb.*, fimbria. *N. o. l.*, nucleus olfactorius lateralis. *Pall.*, pallium. *Rec. preop.*, recessus preopticus. *S. l. i.*, sulcus limitans internus. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

Zona limitans medialis is very clearly defined, particularly in the caudal part of the hemisphere (fig. 13, *Z. l. m.*). Approximately horizontal in the rostral part, it assumes a vertical position at foramen monroi. Its position is especially worthy of notice in relation to sulcus limitans internus, as it does not run straight out towards this groove at the wall of the ventricle but immediately dorsal to the groove, which thus runs in the ventral border of zona limitans. This circumstance is most noticeable in the caudal parts of the hemispheres, where zona limitans is broad close to the ventricle as well.

The fimbrial part of the septum has become larger, those parts of nucleus lateralis septi stretching dorsally to foramen monroi are at this stage already fairly important. Of the septum nuclei, the lateral is the larger, extending practically through the entire hemisphere (fig. 13, *Nucl. l. s.*). It separates from the ventricular cell-layer just below sulcus limitans internus. On a series of transverse sections the nucleus is seen to begin somewhat behind the sections on which the accessory bulbs are found, i. e. in the rostral border of the hemisphere proper. — As stated above, nucleus medialis septi (fig. 13, *Nucl. m. s.*) separates from the granular cells in bulbus olfactorius, from whence the cells extend medially right up to the wall of the brain caudad and upward through the subpallial parts of the septum. This nucleus has not yet at the 3,5 cm. stage extended through the whole septum, nor as far as foramen monroi. The difference between the cells in the lateral and the medial septum-nuclei is considerably (fig. 15), as might be expected from their originating in such different cell areas. The lateral cells are large, although smaller than the pallial cells, and compose small groups of longitudinal form, lying one beyond the other between the ventricle and the medial wall of the brain. These cells are mostly round in form. The cells of the medial nucleus are decidedly inferior in size to those of the lateral nucleus, do not stain so darkly and are elliptic in form; they are all disposed along the medial septum wall and in a dorso-ventral direction.

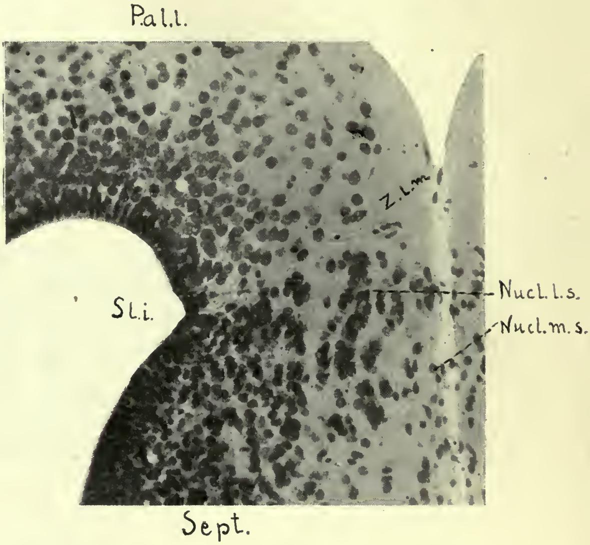

Fig. 15. Rana, 3,5 cm. Cross section, pallium, zona limitans and the dorsal part of septum. *Nucl. l. s.*, nucleus lateralis septi. *Nucl. m. s.*, nucleus medialis septi. *Pall.*, pallium. *Sept.*, septum. *S. l. i.*, sulcus limitans internus.

The lateral wall of the hemisphere is in process of reduction, although as yet considerably more powerful than in the adult frog. The lateral part forms, as already stated, two ridges running to the ventricle on each side of groove *G* (fig. 13). The ventricular cell-layer is here unusually rich and is separated from the peripheral cells by fissurelike formations resembling those found at earlier stages. The dorsal ventricular is the more powerful of these two parts. Outside the two inner cell areas we find two outer areas of cells rostrally separetad from each other by a narrow cell-free segment. From the dorsal area the cells descend in a point towards the outer surface of the brain. On a level with foramen monroi a part of the ventral lateral nucleus is seen differentiating from it forming a small round nucleus close to the cell-free part embodied in the lateral forebrain tract, with which this small nucleus appears to be connected.

Stages with developed forelegs (near the metamorphosis). — The brain now begins to resemble that of the adult frog, both in form and in disposition of cells. The lateral ventricles are long and narrow (fig. 16) except in the proximity of foramen monroi. In the bulbous part, where they extend in towards the granular cells, they are at first transverse fissures, their corners formed medially by the ventral floor groove *C*, and laterally by groove *G*. A dorsal groove soon appears, which a short distance caudad gives the ventricle a triangular form on the transverse section. Groove *G* becomes shallower, the medial part bends downward and the ventricle becomes a dorso-ventrally situated fissurelike formation. Sulcus limitans internus becomes visible approximately where the ventricles change from the triangular to the oblong form.

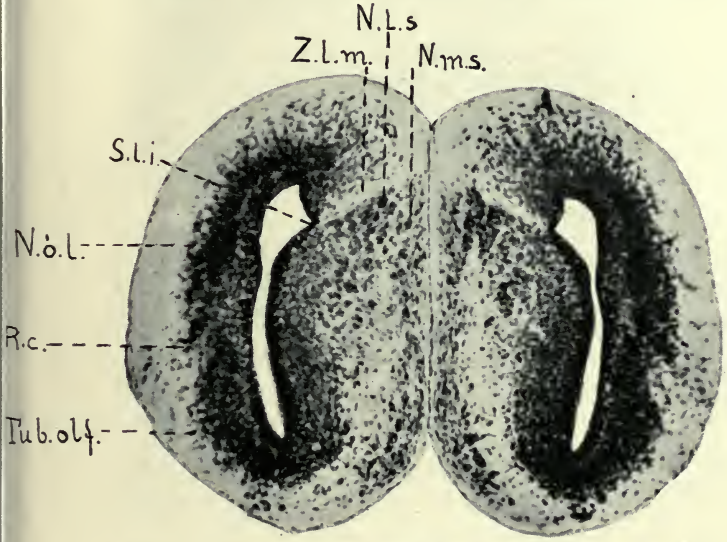

Fig. 16. Rana, a stage near the metamorphosis. Cross section. *N. l. s.*, nucleus lateralis septi. *N. m. s.*, nucleus medialis septi. *N. o. l.*, nucleus olfactorius lateralis. *R. c.*, regio curva. *S. l. i.*, sulcus limitans internus. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

The medial wall of the brain is thicker than the lateral. The two septal nuclei have developed vigorously. The medial nucleus (fig. 16, *N. m. s.*) lies like a powerful multistratal cell area along the medial surface of the hemisphere from the ventral side right up to zona limitans medialis in the central part of the hemisphere. Further caudad it does not extend so far up; the fimbriate nuclei, now large in size, are still only formed from the lateral septal nuclei. — Zona limitans medialis is clearly visible immediately behind the commencement of sulcus limitans internus, originating simultaneously with the lateral septum nucleus; it does not at first stretch in towards the ventricle, but only separates the peripheral cell-parts from each other. Further caudad it runs right in towards sulcus limitans internus, but its inner section is extremely narrow. It becomes continually broader and more fully developed as it advances caudally; as already indicated at the preceding stages, it there descends towards the ventricle dorsal to sulcus limitans internus.

In the lateral wall of the hemisphere the cell part situated ventrally to groove *G* and the projecting cell-wedge (*R. c.*) is that which has become most reduced (fig. 16). The outer cell-layer is more powerful furthest frontad towards formatio bulbaris; more caudally it becomes sparser and diminishes also dorso-ventrally in circumference, ending at foramen monroi in the above-mentioned small round nucleus. At this stage, however, the said nucleus is considerably larger in circumference than before. The dorso-lateral nucleus is fairly large, in the anterior part of the brain it extends in front of the dorsal part of the lateral ventricle and stretches in towards the medial side (fig. 17) to the cell group formed of the rostral part of the pallium. Caudally it extends behind foramen monroi and ends in the occipital lobe.

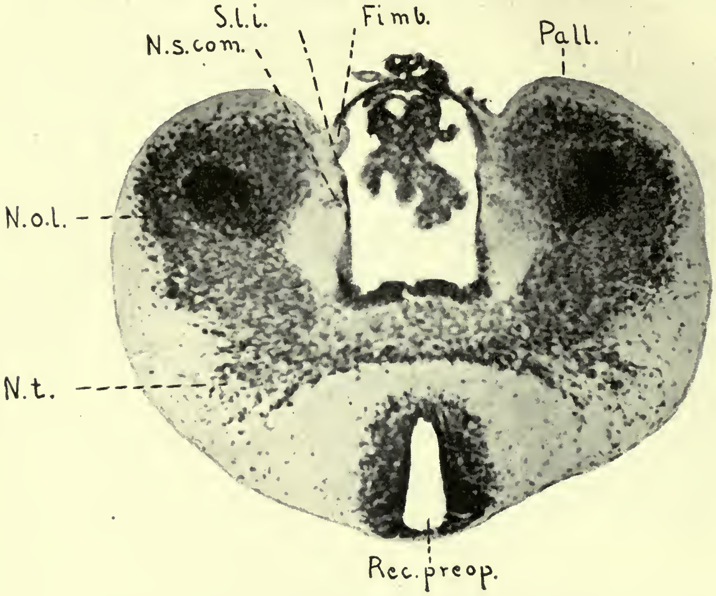

Fig. 17. Rana, cross section through the same brain as in fig. 16. Caudal part of the forebrain. *Fimb.*, fimbria. *N. o. l.*, nucleus olfactorius lateralis. *N. s. com.*, nucleus supracommissuralis. *N. t.*, nucleus tæniæ. *Pall.*, pallium. *Rec. preop.*, recessus preopticus. *S. l. i.*, sulcus limitans internus.

The pallial part situated dorsally and medially to the lateral ventricle, is practically quite filled with cells, radially disposed towards the ventricle. In the periphery they lie rather sparsely scattered along the surface of the hemisphere, inwards they lie more closely packed and have their longitudinal axe directed towards the ventricle. The remainder of the ventricular cell-layer is composed only of a layer of ependymal cells.

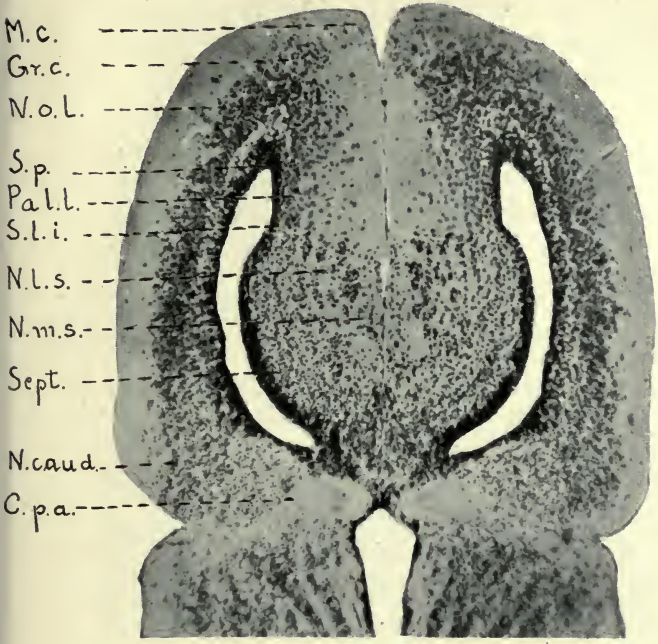

Fig. 18. Rana, a stage near the metamorphosis. Horizontal section ventral to the foramen monroi. *C. p. a.*, commissura pallii anterior. *Gr. c.*, granule cell layer of the olfactory bulb. *M. c.*, mitral cell layer of the olfactory bulb. *N. caud.*, nucleus ventralis striatici (nucleus caudatus; Johnston). *N. l. s.*, nucleus lateralis septi. *N. m. s*, nucleus medialis septi. *N. o. l*, nucleus olfactorius lateralis. *Pall.*, pallium. *Sept.*, septum *S. l. i*, sulcus limitans internus. *S. p.*, sulcus prepallialis.

Rostrally the pallial cells extend far down through the medial wall, so that in a series of horizontal sections part of the pallium lies in front of the subpallial parts of the septum and its nuclei (fig. 18). Dorsally in front of this pallial part we find the above mentioned medial part of the dorsolateral nucleus; more ventrally the granular cells extend frontad at this stage towards the pallium part. No dorso-ventrally directed grooves are as yet seen to have developed in the rostral part of the lateral ventricle, the boundaries between the different groups of cells surrounding it are however distinctly defined by the varying types of cells found in them.

THE FOREBRAIN OF THE FULLGROWN FROG SEEN IN THE LIGHT OF ITS EMBRYONIC DEVELOPMENT.

A careful investigation of the frogbrain in its embryonic stages seems to lead to a conception of the same differing in a great degree from that which has hitherto been accepted. Edinger was the first to point out that the brain of Amphibia is at an embryonic stage and the simplest in structure among the vertebrates. This statement has since been repeated by practically every investigator of the amphibian brain belonging to Edinger's school. The most cursory glance at one or two stages of the embryonic frogbrain shows, however, that in regard to telencephalon, Edinger's statement is without any real foundation. If the forebrain of the frog had really an embryonic character it would follow that after the formation of the hemispheres had taken place, it would have undergone only very slight development, or even remained at an embryonic stage. This is, however, by no means the case, the difference in the forebrain of e. g. a 1,2 cm. frog-larva and an adult frog being so great, that it is hardly possible to suppose they belong to the same species. The telencephalon is far from remaining at an embryonic stage, certain parts having undergone extremely vigorous reduction, while other parts, on the contrary, are singularly slightly developed in the embryo, and only arrive at complete development in the full-grown individual. It is only by tracing the development of telencephalon in the frog-embryons, stage by stage, as has been done in this case, that it becomes possible to obtain a well-founded idea of its morphology.

The pallial parts. — It is possible to distinguish a number of grooves on the surface of the telencephalon already at an early embryonic stage before the lateral ventricles have begun to develope. On the outer dorsal surface the groove indicated with the letter *E* is visible, on the inner ventricular surface grooves *B* and *C*. Grooves *E* and *B* together form the boundary of the dorsal part of the lateral plates, which lies medial to the dorso-lateral cell-free section (fig. 5). Groove *B* may be traced through practically all stages of development. After the evagination of the lateral ventricles it forms a lateral boundary-groove within the same. Groove *E*, on the other hand, disappears fairly early. The cells situated dorsally and medially to these two grooves differ considerably in disposition and appearance from those ventral to them. I consider that this cell-area, so well-defined in frog-embryons, forms the pallial part of the telencephalon in this species; thus I homologize groove *B* with the sulcus limitans pallii of other vertebrates; the outer groove *E* I consider homologous with the fissura endorhinalis externa of reptiles, which in the latter forms an outer boundary-groove for the pallial parts. In tadpoles, as in reptiles, this groove frequently is continued by a set of blood-vessels, which force themselves into the telencephalon in a position corresponding to that held by the groove. The above-mentioned well-defined pallial area is considerably less in circumference than that part of the forebrain previously designated as the pallium, which at the embryonic stages extends right down to the groove marked *G* (fig. 8). In the adult frog sulcus limitans pallii runs somewhat ventral to the dorsal border of the lateral ventricle. It is true that the groove itself is here indistinct, but the differences in cellstructure, which at the embryonic stages are found on either side of the same, remain; there is no difficulty in pointing out the position of the lateral boundary-groove and boundary-zone between the pallial and subpallial areas. A fully developed cell-free zona limitans lateralis cannot, however, be found in either embryos or adult animals. — Thus, the dorso-lateral cell-free area at the outer wall of the brain (fig. 5, *d. l. c. a.*), which has been described at the embryonic stages, is situated ventral to the pallium; it appears as has already been stated, to be originally formed of olfactory fibres, which give rise to tractus olfactorius lateralis, this tract thus traversing the subpallial region in analogy with what is the case in other lower vertebrates. The pallium developes most vigorously in a medial direction, till it forms a powerful part completely filled with cells. Two cell-layers, an inner ventricular one and an outer cortex, composed of newly-formed cells migrating from the inner layer, may be distinguished in the pallium as well as in other parts of the forebrain at the earlier embryonic stages (fig. 9). This form of development for the cortex is in full agreement with that which, according to Professor HOLMGREN, gives rise to the primordial cortical layers in sharks. Thus, at earlier stages, it is quite possible to distinguish a cerebral cortex clearly separate from the ventricular cell-layer. This cerebral cortex, however, never arrives at such a degree of development in the adult frog, that a compact cell-mass can be distinguished. On the contrary, this rudimentary cortex appears to become reduced by degrees and to merge into a cell-mass consisting of fairly sparsely scattered cells, situated between the ventricle and the outer surface of the brain, where, however, the outer cells have retained the position, parallel with the outer surface of the brain, which is characteristic for the migrated cortex parts, and where the remaining cells are disposed radially towards the wall of the ventricle. — The medial limits of the pallium, zona limitans medialis and sulcus limitans internus, originate simultaneously with the beginning development through evagination of the hemispheres. In Amphibia the pallium never extends in a ventro-medial direction below zona limitans medialis, this boundary is from the beginning so well-defined and the cells on either side of it so clearly separated from each other, that there can be no question of assigning parts situated ventrally to it to the pallium, as JOHNSTON has done with the so-called fimbria and the nuclei from which they are formed. There is as little foundation for the view held, formerly at least, by ELLIOT SMITH, that primordium hippocampi developes from the fimbria and thus is a subpallial part.

As the medial part of the forebrain becomes its position through evagination of the lateral plates, there theoretically may exist a primary connection between the medial and lateral structures of the frontal telencephalic parts. The two ventricular boundary-grooves between the pallium and the subpallium are thus strictly speaking only one groove, i. e. sulcus limitans pallii, which through the anterior part of the telencephalon having become bent into the original medial ventricle (fig. 6), continues along the medial side. It is possible to prove a direct connection between the two grooves even in older frogs, although the rostral part of the telencephalon has then undergone great changes through the vigorous development of the olfactory bulbs situated there. Sulcus limitans internus is in adult frogs and older embryons continued in the rostral part of the lateral ventricle by a groove named by GAUPP sulcus præpallialis (figs. 18 and 19, *S. p.*), which thus runs obliquely up trough the ventricle to the dorsal edge of the same. A similar proceeding may be noticed laterally in sulcus limitans pallii, which also rises upward to the upper corner of the ventricle, where it converges on the medial groove. Thus these two grooves bound the pallium rostrally as well as ventrally; the rostrally situated bulbus olfactorius part of telencephalon is consequently an entirely subpallial part. At the stages where the hemispheres have newly begun to form and the bulbus rudiments remain partly in their original position, it should be easy to show the connection between the two boundary grooves, especially as sulcus limitans pallii is then very distinct, but the anterior part of the ventricle is so compressed, that it is difficult to prove this fact. It is, however, possible to trace both these grooves rostrally into the ventricle, one on each side, till the latter becomes extremely small. A connection probably exists between them. Sulcus limitans pallii originates at the base of the anterior epithelial membrane at the lateral plate, this membrane still remains at the evaginated stage, uniting the two inward-curving lateral plates; it is possible to trace sulcus limitans internus in a caudal direction up to this base of the membrane, thus it has the same starting-point as the outer pallial boundary-groove before evagination has taken place, which fact also points to both grooves being traceable to the original sulcus limitans pallii.

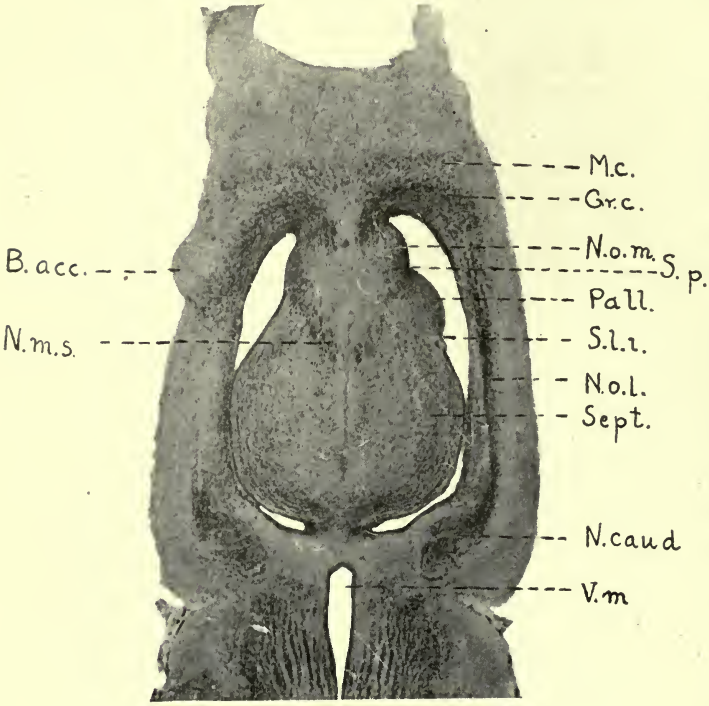

Fig. 19. Rana, adult. Horizontal section ventral to the foramen monroi. *B. acc.*, bulbus accessorius. *Gr. c.*, granule cell layer of the olfactory bulb. *M. c.*, mitral cell layer of the olfactory bulb. *N. caud.*, nucleus ventralis striatici (nucleus caudatus; Johnston). *N. m. s.*, nucleus medialis septi. *N. o. l.*, nucleus olfactorius lateralis. *N. o. m.*, nucleus olfactorius medialis. *Pall.*, pallium. *Sept.*, septum. *S. l. i.*, sulcus limitans internus. *S. p.*, sulcus praepallialis. *V. m.*, ventriculus medialis.

Three distinct parts may be distinguished in the pallium of the adult frog: a medial hippocampal pallium, a dorsal general pallium and a lateral pyriform pallium. Of these the hippocampal and the pyriform pallium extend furthest frontad. In reading a series of transverse sections in a caudal direction, the general pallium is seen wedging itself in between these two parts. Caudal the pyriform and general pallium extend furthest, stretching out into the most caudal part of polus occipitalis. The hippocampal pallium ends somewhat caudal to foramen monroi, where its two boundary-grooves converge.

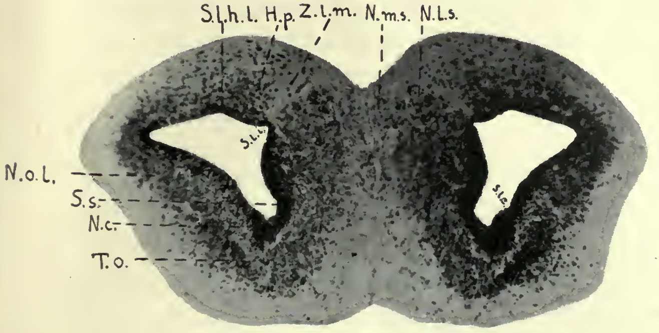

Fig. 20. Larva of a south-american tree-frog. Cross section. *H.p.*, hippocampal pallium. *N. c.*, nucleus ventralis striatici (nucleus caudatus; Johnston). *N. l. s.*, nucleus lateralis septi. *N. m. s.*, nucleus medialis septi. *N. o. l.*, nucleus olfactorius lateralis. *S. l. e.* sulcus limitans externus. *S. l. h. l.*, sulcus limitans hippocampi lateralis. *S. l. i.*, sulcus limitans internus. *S. s.*, sulcus septalis. *T. o.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

Dorsally along the ventricle the hippocampal pallium is bounded by a horizontal groove, sulcus limitans hippocampi lateralis. In Rana, this groove is well-defined only in the full-grown individual; in older larvae, a faint indication of the commencing groove may be observed. In other species of Anura this pallial groove is already distinct at the larval stage, this is the case in Pipa and a species of South-American tree-frog, which I have investigated (figs. 20 and 22, *S. l. h. l.*). The ependymal cell-layer in the hippocampal area is very thin, differing in this respect from the ependymal layer which surrounds the rest of the ventricle. The ganglion cells of this part of the pallium are large and fairly round in form. With chresylviolet they stain lighter than the other pallial cells. The cells lie thinly scattered between the ventricle and the surface of the brain, but somewhat more closely packed towards the ventricle, where they are partly disposed in rows, parallel with its surface. The outer cells are radially disposed towards the ventricle.

In the general pallium the ependymal cells lie closely packed. The peripheral cells are elongated, considerably smaller than the hippocampal cells, and appear darker than the latter on sections stained with chresylviolet. The radial disposition of the cells towards the ventricle is more striking here than in the hippocampal part. The cells here also extend to the surface of the brain.

The dorsal boundary of the pyriformal pallium converges approximately on the dorsal corner-groove of the ventricle. The cells here are considerably less differentiated, and are more closely packed towards the ventricle. The outer cells do not extend to the surface of the brain, the inner are found aggregated in a couple of cell-plates close to the ventricle. The radial disposition of the cells may again be observed in this part of the pallium. In the matter of form and impregnability the cells of the pyriformis part correspond with those of the general pallium.

The subpallial parts. — The subpallial, as well as the pallial parts are originally connected in the rostral part of the telencephalon, but during the process of development they become partly separated in consequence of bulbus olfactorius, which was originally situated laterally having been forced frontad towards the rostral edge of the brain, simultaneously with the increase of the latter in size.

The lateral parts of the subpallium are those which are best developed at the embryonic stage; they are considerably more powerful than the medially situated parts of the septum. That part of the forebrain situated to sulcus limitans pallii is divided by the groove, which at the larval stage was designated by the letter *G*, into a dorsal and a ventral part. This is the groove which in other vertebrates is known by the name of sulcus limitans externus or lateralis, it is already developed at the early embryonic stages (fig. 4). In the adult animal it may be traced from the region of foramen monroi caudad to the anterior part of the lateral ventricle, where it runs beside the dorsal edge of the granular cell-layer. Here it rises towards the upper corner of the ventricle, parallel with the sulcus limitans pallii, crosses over, in like manner, to the medial side of the ventricle and continues there as a groove, called by Gaupp Sulcus prælimbicus, which forms the boundary between eminentia postolfactoria (Gaupp) and the granular cells in bulbus olfactorius. That part of the subpallium which in the adult frog is bounded by sulcus limitans externus and the pallial boundary-groove is nucleus olfactorius lateralis. Thus this nucleus also extends to the medial side in the rostral part of telencephalon, rising on the dorsal side of the ventricle simultaneously with its boundary-grooves in the anterior part of the ventricle, to drop again later on the medial side, where, in front of the septum, it forms a section that curves inward to the ventricle. This is eminentia postolfactoria (Gaupp), which should by rights be called nucleus olfactorius medialis (fig. 19, *N. o. m.*). The continuation in this manner of a lateral part of subpallium on the medial side of the brain, would appear to be a consequence of the evagination of telencephalon. Its further penetration in a caudal direction on the medial side is, however, hindered by the powerful development of the septum parts. Outside the nucleus olfactorius lateralis lies the tractus olfactorius lateralis, which follows the nucleus from its most rostral part to polus occipitalis, where the tract passes over through stria medullaris into commissura habenularis. The olfactory tract originates in the anterior part of the telencephalon, where some fibres are running laterally and giving rise to the lateral olfactory tract, others medially, giving rise to the medial olfactory tract. This tract, which Snessarew (1908) was the first to describe correctly, runs down on the medial side of the hemisphere, following in its course the medial olfactory nucleus down towards the ventral side of the forebrain. Behind this nucleus the tract runs down towards the ventro-medial corner of the hemisphere, continuing there caudally to the region of foramen monroi, where it rises on the lateral side to unite with the lateral olfactory tract and with it merge into the habenular-commissure.

The lateral olfactory nucleus appears in the adult frog as a faint curved cell-mass, with its concavity pointing in the direction of the surface of the brain; it extends from the ventral edge of the pallium, where it projects slightly from the ventricle, down into the part called regio curva. The cells in the olfactory nucleus differ from the pallial cells, appearing to have migrated in flocks, whereas the pallial cells are radially disposed.

This part of the telencephalon was formerly called lobus pyriformis (HERRICK) or paleopallium (KAPPERS and others) and was thus regarded as a pallial part. As the pallial boundary according to my opinion in frog-embryons must be placed dorsal to this nucleus it cannot be a pallial part. By comparing the frogbrain with that of other lower vertebrates and reptiles, I have found that there is a striking resemblance between the nucleus olfactorius lateralis in these animals and this nucleus in the frogbrain, not only as to its position and development but also concerning its fibre connections. In the telencephalon of sharks and Chimaera as well as of bony fishes and Protopterus there is found a nucleus situated between the zona limitans lateralis and the tuberculum olfactorium. In those types having an inverted forebrain that nucleus lies medial to the lateral olfactory tract. The nucleus olfactorius lateralis in sharks develops in the same way as this nucleus in the frogbrain. Thus in the latter nucleus I see an homologon to the nucleus olfactorius lateralis, which has not before been recorded from the amphibian forebrain.

As has already been pointed out, the lateral wall of the hemisphere is particularly well developed in the frog-larva. Here, as in the pallium, an inner ventricular layer of cells may be distinguished from an outer migrated cortical layer (fig. 7). These cell-layers are in their turn subdivided into a dorsal and a ventral part by sulcus limitans externus (*G*). The inner cell-layer appears in these frog-larvae to represent a subpallial part of the brain, viz. corpus striatum. These striatal parts are, however, subjected to such powerful reduction during embryonic development, that they have almost entirely disappeared in the full-grown frog. Outside the dorsal striatal region an outer cell-layer differentiates at the larval stage (fig. 11, *N. o. l*), giving rise to the nucleus olfactorius lateralis described above; ventrally a cortical-like part differentiates (*tub. olf.*), presenting a striking resemblance to tuberculum olfactorium, not only in the way it originates, but also in appearance (figs. 20 and 21). It is well-known that tuberculum olfactorium is found fully developed in selachians and Dipnoi as well as in reptiles. GAUPP has pointed out that the part of subpallium which he calls pars angularis, might be homologous to the area olfactoria of reptiles; I know of no other investigator who has attempted to discover a tuberculum olfactorium in the frogbrain. In larvae this cell region lies like a typical bowl-shaped formation, surrounding the ventral striatal area. When striatum becomes reduced in the process of development, the parts situated outside this embryonic region are in consequence again drawn in towards the surface of the ventricle, thus, both the lateral olfactory nucleus and the ventro-lateral nucleus are found in a ventricular position in the full-grown frog. I therefore consider that part of subpallium lying between regio curva and the lower edge of the ventricle as tuberculum olfactorium in Rana. — Tuberculum olfactorium continues caudally behind foramen monroi in a small round nucleus, situated ventro-laterally to the lateral ventricle. As in the case of tuberculum olfactorium, this nucleus is most clearly defined in the larval stages (fig. 17, *N. t.*). It is, as is also the case with tuberculum olfactorium, particularly well developed in the larvae of Pipa, and of the above-mentioned American tree-frog (fig. 22). As this nucleus, in regard to fibre-connections as well as to its position and its connection with tuberculum olfactorium appears to correspond with the nucleus tæniæ of sharks, and Dipnoi, I must pronounce it homologous with the latter nucleus.

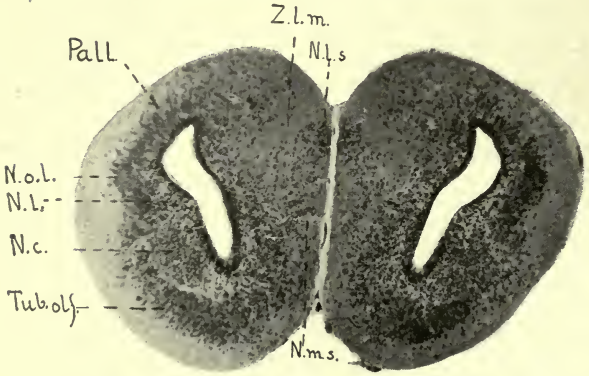

Fig. 21. Pipa, larva. Cross section through the anterior part of the forebrain. *N. c.* nucleus ventralis striatici (nucleus caudatus; Johnston). *N. l. s*, nucleus lateralis septi. *N. l.*, nucleus dorsalis striatici (nucleus lentiformis; Johnston). *N. m. s.*, nucleus medialis septi. *Pall.*, pallium. *Tub. olf.*, tuberculum olfactorium. *Z. l. m.*, zona limitans medialis.

Striatum has in the adult frog been increased by a third caudal part, which developes only at the later larval stages. This caudal striatum part lies along the lower edge of the ventricle, partly medial to the nucleus tæniæ. In the adult specimen it also extends somewhat medially to the ventricle, and is then separated from the septum by a groove. Rostrally this region is also bounded by a vertical groove, which may be observed in older larvae. This part of striatum becomes concentrated behind foramen monroi in a compact nucleus, the anterior part of which lies ventro-medially to nucleus tæniæ. As already stated, its anterior part is covered by tuberculum olfactorium, as is the case with part of the nucleus caudatus (JOHNSTON) in reptiles, with which it also appears to correspond in regard to position.[1] The nucleus caudatus of reptiles extends, it is true, considerably further in a rostral direction than is the case with this caudal striatal part, I consider, however, that the ventral swelling of the striatum, described at embryonic stages, is a rostral part of this nucleus, which in the adult frog only survives as a ventricular cell-layer. In the embryons of Chrysemys, a rostral part of nucleus caudatus (Johnston) may be distinguished, situated close to the ventricle and differentiating into two parts at foramen monroi. The dorsal part extends some distance into the posterior lobe of the hemisphere, the ventral running down into telencephalon medium and extending there to the upper part of nucleus preopticus. This extension of nucleus caudatus agrees so well with the striatum nucleus in Rana described above, that I do not hesitate to homologize these nuclei. In Rana the nucleus ventralis striatici is frontally not deliminated from the ventricular layer and therefore in this part cannot be considered as quite corresponding to the nucleus caudatus (Johnston) in reptiles. In Pipa-embryons, however, the head part of the nucleus ventralis striatici is quite free from the ventricle and basally covered by the tuberculum olfactorium (fig. 21, *N. c.*). This structure in Pipa-embryons having a cortical arrangement more or less as in reptiles makes the resemblance of these structures in Pipa and reptiles very striking. The head of the nucleus ventralis striatici in Pipa-larvae posteriorly becomes connected with the ventricular wall and is to be followed caudally as a thin cellular band which at the foramen monroi merges with the nucleus called by Herrick the amygdalus-nucleus. In amphibians the nucleus in question thus seems to correspond to the tail of the caudate in reptiles forming part of the amygdala. Herrick has namely described the corresponding nucleus as amygdala on account of its fibre-connections and of its function. Johnston (1915) comprises the following parts of the turtlebrain in an amygdalus-complex: nucleus olfactorius lateralis, the tail of nucleus caudatus, the medial large-celled nucleus and probably part of the dorsal ventricular ridge. According to these writers, nucleus caudatus thus forms a part of amygdala, although, as Herrick points out, it cannot be entirely homologized with so simple a nucleus as nucleus caudatus appears to be in the Anura. The nucleus which Dart (1920) terms nucleus

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[1] To the tuberculum olfactorium in reptiles I thus include the substantia perforata anterior, as a caudal part without cortical arrangement (islands of Calleja).

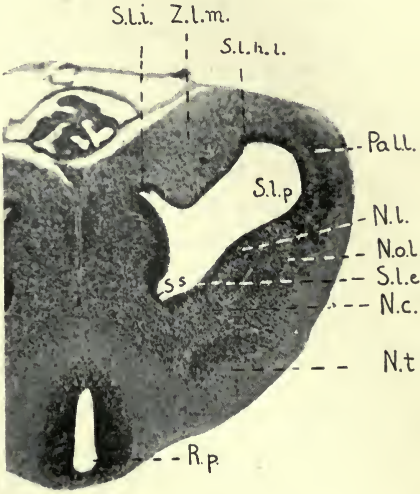

Fig. 22. Pipa, larva, the same series as in fig. 21, cross section behind the foramen monroi. *N. c.*, nucleus dorsalis striatici (nucleus caudatus; Johnston). *N. l.*, nucleus ventralis striatici (nucleus lentiformis; Johnston). *N. o. l.*, nucleus olfactorius lateralis. *N. t.*, nucleus tæniæ. *Pall.*, pallium. *R. p.*, recessus praeopticus. *S. l. e.*, sulcus limitans externus. *S. l. h. l*, sulcus limitans hippocampi lateralis. *S. l. i.*, sulcus limitans internus. *S. l. p.*, sulcus limitans pallii. *S. s.*, sulcus septalis. *Z. l. m.*, zona limitans medialis.

amygdalus proprius in reptiles, is not identical with the nucleus in Amphibia described above, it is of pallial origin, thus corresponding with another part of the amygdalus-complex in mammals than nucleus caudatus (Johnston).

In my opinion, the striatum in the frog thus consists firstly of a rostral area, which during the embryonic stage is a fairly powerful part, divided by a horizontal groove into an upper and a lower part, secondly, of a caudal area. A portion of the dorsal part might possibly be homologous with nucleus lentiformis (Johnston) (fig. 21, *N. l.*), the ventral forms part of nucleus caudatus (Johnston) (*N. c.*). This rostral area becomes reduced during development, a posterior part developing at the same time from nucleus ventralis striatici, which thus in the full-grown frog represent the remaining independent part of the striatum, the rest merging with the tuberculum olfactorium and the nucleus olfactorius lateralis at the ventricular wall.

Kappers, de Lange and Röthig have placed an epistriatum immediately ventral to sulcus limitans externus, i. e. in that part of telencephalon assigned by them to the subpallium. De Lange considers that epistriatum is formed from striatum, Kappers, however, contests this view in his newly published work: "Vergleichende Anatomie des Nervensystems." It does not appear to me that there is any reason to try to homologize any part of the brain of the Amphibia with the epistriatum of reptiles; should such a part of the brain exist, it would have to be sought within the pallium region, and thus dorsally to sulcus limitans pallii.

That part of the subpallium situated medially to the lateral ventricle and ventrally to zona limitans medialis, is in the adult frog the most powerfully developed part of the hemisphere. This part is variously designated as corpus precommissurale, paraterminal body and septum; I adopt the last mentioned term. The septum extends in a caudal direction from the caudal boundary of the granular cell-layer of the bulbus region, through the ventro-medial part of the forebrain to nucleus preopticus. In frog-larvae this part of telencephalon is the last to develope. A considerable time elapses after the commencement of evagination before an actual septum part can be observed. The ventricles are divided from the outer surface in a medial direction only by a thin membrane, which may be compared with that which in urodeles goes by the name of septum ependymale. A powerful pallium forms an arch over this membrane, and ventral to it is seen the massive basal part which later assists in forming the septum (fig. 10). Ventral to the base of the abovementioned membrane, and thus exactly below the boundary of pallium, the lateral septal nucleus begins to differentiate from the ventricular cell-layer (fig. 11, *N. l. s.*), which lies in the posterior border of the newly formed septum. The nucleus increases in size with remarkable rapidity, new cells ceaselessly migrating from the ventricular layer. It increases partly in a rostral, partly in a caudal direction, extending medially almost to the surface of the hemisphere, till it at last forms that part of the septum which borders on zona limitans medialis (fig. 15). Its vigorous increase in a caudal direction causes it to force this boundary-zone from its original horizontal position, rising its medial part upwards till it finally occupies an almost vertical position. Through the caudal expansion of nucleus lateralis septi, it finally presses past foramen monroi, dorsally to the latter, thus giving rise to pars fimbrialis septi (figs. 12 and 14). — The medial septal nucleus originates from the granular cell-layer of bulbus olfactorius, being thus formed of the rostral ventral part of the subpallium, increases in a caudal and dorsal direction during the development of the brain, till in older animals it is found as a powerful nucleus stretching through the whole of the septum along its medial surface (fig. 16) and finally, in the adult frog, extends right into pars fimbrialis septi. This septal nucleus appears to be homologous with the nucleus which in teleosts is termed nucleus olfactorius anterior pars præcommissurale, which is also derived from the bulbous part of the brain, a fact pointed out by Professor Holmgren (1920).

If we accept Johnston's view that the fimbrial nuclei must be assigned to the pallium, the boundary of the latter would have to be drawn as far down as bulbus olfactorius, since the nuclei forming the fimbrial part of septum extend through the greater part of the latter. The embryonic origin of the fimbria, however, clearly proves the subpallial source of these parts, the position of foramen monroi originally also coincides with that occupied by zona limitans medialis, the parts lying dorsal to foramen monroi being thus pallial, those situated ventrally being subpallial. The fimbria are thus entirely secondary formations, and their dorsal position is only a consequence of the rapid growth of the septum during a later period of the development of telencephalon.

In addition to the lateral and the medial septal nucleus, a powerful ventricular cell-layer is found in septum, which developes during the later larval stages. The cells lie disposed in compact rows along the wall of the ventricle, hereby differing from the cells in nucleus olfactorius medialis, situated ventrally to the rostral part of the septum. These cells, however, lose their stratal order in the peripheral area, where they lie diffusely scattered frontad towards the nucleus medialis septi. The cells from the two parts of septum unite in the rostral part of the commissural-bed, forming a ventricular nucleus, situated in front of commissura hippocampi, ventral to foramen monroi.

In the caudal part of septum, a vertical groove may be distinguished running between that part of septum which forms the fimbria and the ventricular part described above. This groove is sulcus septalis (figs. 20 and 22, *S. s.*), which in sharks and Dipnoi divides the septum into two parts, a dorsal and a ventral, the former composing the fimbrial part. The two parts of septum are in these animals of approximately the same size, the region from which nucleus lateralis septi is formed being larger than in frogs. As above mentioned, nucleus lateralis septi is formed during embryonic development from the area situated close to foramen monroi. The great expansion of the nucleus in the full-grown animal depends upon the migration of its cells from this small ventricular area, which in the adult individual still retains its position close to foramen monroi, and is there bounded ventrally by sulcus septalis.

Pars medialis telencephali is composed of the ventral part of the forebrain, situated behind foramen monroi, it extends caudally to the boundary of diencephalon, i. e. if JOHNSTON's view be accepted, dorsally to velum transversum and ventrally to the chiasma-ridge. The lateral portions of this part of the brain are filled with fibre-masses, chiefly the medial and the lateral forebrain tracts. The medial part is filled by the nucleus preopticus which surrounds the preoptical ventricle. Along the lateral walls of recessus preopticus it is possible already at early embryonic stages to distinguish a groove, running diagonally through the ventricle from the anterior dorsal down to the caudal ventral corner. Along this groove lies a group of cells, which differ by their size from the other cells in nucleus preopticus. These cells are most numerous close to the dorsal part of the ventricle, where they spread out, forming a cell-plate, which later juts down, skirting the above-mentioned groove among the smaller preoptic cells, and extending down to the lower edge of the chiasma. These two nuclei are clearly homologous with those in teleosts described by various authors: nucleus preopticus pars parvocellularis and nucleus preopticus pars magnocellularis.

Rostral to the lateral and medial olfactory nucleus and the ventral part of septum, lies bulbus olfactorius. Its granular cell-layer extends to the most frontal part of the lateral ventricle. The granular cells are basally connected with nucleus medialis septi. The original position of bulbus olfactorius is, however, not rostral but lateral, as has been pointed out in the account of the embryonic stages. It has been previously asserted by ELLIOT SMITH (1910) that the bulbous formation lies exactly rostral to primordium hippocampi and that this was its original position, for which reason it has been used as a criterion for this part of the pallium. The conditions in the frog, however, clearly show that the pallium, at the embryonic stages, extends in front of and dorsal to bulbus, which only at a fairly late stage takes up its final position in the rostral part of the hemisphere. Consequently the fusion between the two bulbi also takes place at later stages. The accessory bulbs retain their position on the lateral side, differentiating from the rostral ones before the latter take up their final position.

DESCRIPTION OF THE TELENCEPHALON IN TRITON-EMBRYONS.

The telencephalon in Triton-embryons at early stages presents considerably more difficulty to the student than that of frog-larvae at a corresponding age, on account of the anterior part of the brain in urodeles exhibiting a powerful curve, which causes some difficulty in finding the suitable direction of the sections. The earliest stage of apparent importance in the development of the forebrain is that at which the larva is 0,5 cm. long. The telencephalon is then situated fully ventrally, and is dorsally covered by the diencephalon and the mesencephalon.

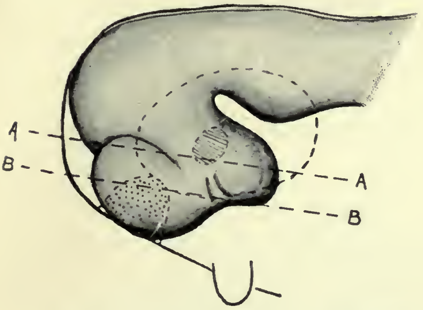

Fig. 23. Triton, 0,5 cm. Reconstruction of the brain, side view. A-A. section shown in fig. 24. B-B. section shown in fig. 25. The dotted area shows the extension of the nasal sac. The dotted line surrounding the striped area shows the extension of the eye and crystal lense.

Herrick (1921) states that in urodeles the evagination of the forebrain first begins in the caudal part, i. e. the caudal lobes evaginate before the anterior portions of the lateral plates, which are situated close to lamina terminalis. This statement appears rather incredible, since evagination clearly begins in the anterior portion of telencephalon in the nearly related Anura. It must also be noticed, that no sign of this so called caudal evagination, visible on transverse sections of Triton larvae at the 0,5 cm. stage, can be observed in somewhat older embryons, while at a still later stage the caudal lobes are seen to be evaginated. The apparent caudal evagination in younger larvae depends in all probability on the position occupied by the telencephalon in the latter. Erroneous determination of the sections has caused the anterior portion of telencephalon to be mistaken for the caudal. It is true that in a reconstruction of the brain of such an embryo an evaginated part is visible, and has been interpreted as a caudal lobe (fig. 23).

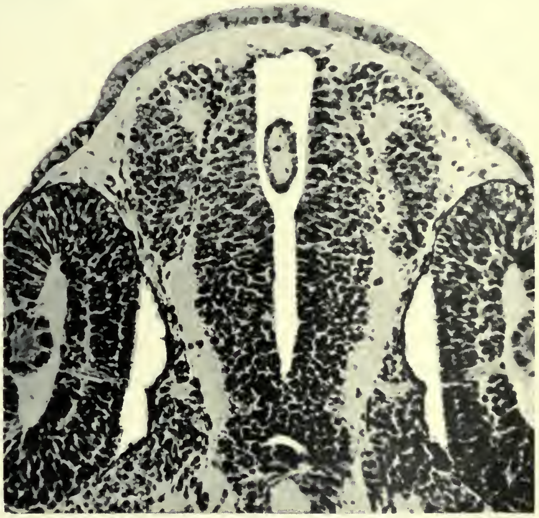

Fig. 24. Triton, 0,6 cm. Horizontal section at the plane A-A in fig. 23.

This is, however, the anterior part of telencephalon, as is clearly evident from, inter alia, the position of the rudiment of bulbus olfactorius. The roof of the forebrain therefore already occupies its normal position, and the continued increase in growth of the brain does not cause the now ventral part to turn upwards as would be the case if the already evaginated portions were the caudal lobes. — Another circumstance that no doubt has contributed to the misconception in respect of a caudal evagination, is that the inversion of telencephalon is at early stages extremely slight. As is the case in the frog-larva, the forebrain consists, to begin with, of two thickened lateral plates, interconnected by an epithelial membrane. The diencephalon in Tritons lying dorsal to these lateral plates, forces them apart, so that they become much further separated dorsally than is the case in Anura, the epithelial roof hereby also becoming wider. A series of horizontal sections of a Triton-larva shows in the dorsal sections, which touch the telencephalon, the picture given in fig. 24. The hemispheres with their evaginated ventricular pouches are found on either side of the medially situated portion of di- and mesencephalon. The membrane dividing the hemispheres medially from the central part is the epithelial roof-membrane. The lateral plates are curved outwards in the caudal part of telencephalon, so that a section cut through their upper portion intersects them as well as the epithelial roof which slopes towards the medial line. Thus a picture of a couple of apparently caudal ventricular pouches is received, bounded on the outer side by the thick lateral plates and inwards by the epithelial membrane. — A section, taken ventrally to that pictured in fig. 24, shows that there is really in this stage of the Triton-larva an anterior evagination (fig. 25). — Herrick (1921) also states that in Dipnoi a similar primary evagination of the caudal lobes is met with; in all probability the same mistake in interpreting telencephalon has been committed here as in the case of the urodeles.

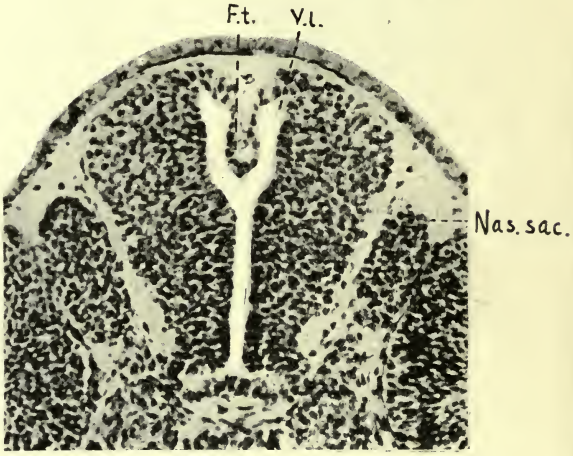

Fig. 25. Triton, 0,6 cm. Horizontal section at the plane B-B in fig. 23. The same series as in fig. 24. *F. t.*, fore-brain tela. *Nas. sac.*, nasal sac. *V. l.*, ventriculus lateralis.

In the 0,5 cm. larva the entire brain remains at the vesicular stage, it should, however, be observed that the medial ventricle, which in Rana-larvae is very wide, is in Triton-embryons reduced to a narrow, almost fissure-like section, surrounded by the extremely thickened lateral plates.

At the 0,7 cm. stage, the hemispheres are already clearly developed with deep and fairly wide lateral ventricles (fig. 26). As shown by the picture they differ considerably from the small round ventricular pouches which develope first in Anura. The medial walls have only become thicker furthest frontad, and are furnished with a multi-stratal layer of ganglion cells. The septum section of the caudal part of the evaginated telencephalon consists only of the anterior epithelial membrane, which here forms a septum ependymale (*s. e.*). Inversion has at this stage progressed so far that the epithelial membrane no longer forms a roof in the caudal part of telencephalon, the latter having through the turning in of the dorsal parts developed into a fold, forming a dorsal continuation of septum ependymale. Inversion continues during the following stages, till finally a fairly powerful pallial part is seen turned down towards the middle line. Inversion is in these older Triton-larvae much more vigorous than in corresponding stages of development in frog-larvae. During the entire embryonic stage a caudal membraneous septum part remains, and is moreover still found in the adult Triton.

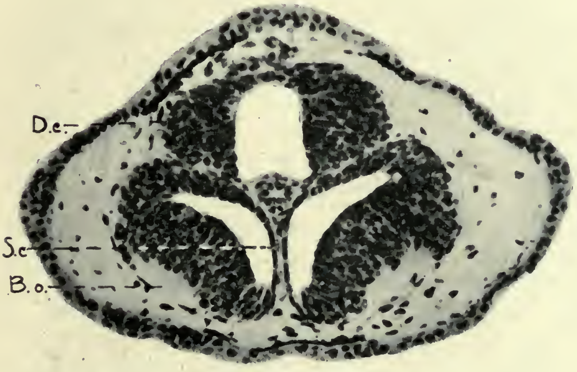

Fig. 26. Triton, 0,7 cm. Cross section. *B. o.*, bulbus olfactorius. *D. e.*, diencephalon. *S. e.*, septum ependymale.

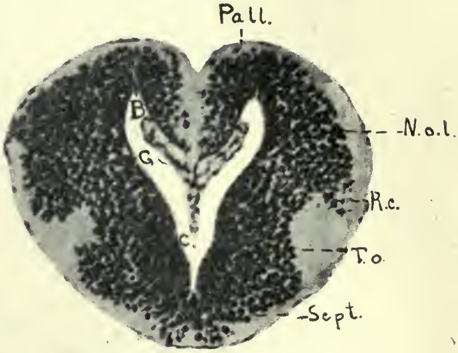

Fig. 27. Triton, 0,9 cm. Cross section behind the foramen monroi. *N. o. l.*, nucleus olfactorius lateralis. *Pall.*, pallium. *R. c.*, regio curva. *Sept.*, septum. *T. o.*, tuberculum olfactorium.

At stages of 0,8—1,0 cm. length, the brain-wall surrounding the medial ventricle is seen to be grooved (fig. 27). A dorsal groove *B* developes through continued inversion and is homologous with groove *B* in frog-larvae, thus forming a boundary between pallial and subpallial parts. Ventral to *B* another groove, *G*, may be seen, which is the striatal groove, viz. sulcus limitans externus. Furthest ventrally groove *C* is visible, dividing striatum from the septum portions of the forebrain.

In the matter of cell distribution the lateral plates in Triton correspond with those in the frog. Thus, at first only a region close to the laterally situated olfactory pits is cell-free, besides an outer dorso-lateral part. The former is the rudiment of bulbus olfactorius, which thus occupies a lateral position in this case as well, the latter is tractus olfactorius lateralis, which begins forcing the ganglion cells away from the surface of the brain. The cells are divided into a ventricular and an outer cell layer, the former having oval, the latter round cells. The difference between the two cell-layers is not quite so distinct as in frog-larvae. The ventricular layer remains rather thin in the dorsal part of the brain, but becomes ventrally considerably powerful during the later embryonic stages. The peripheral portions of the forebrain in the Triton-larva become cell-free rather rapidly. Thus, while a larva of 0,8 cm. length has its brain filled with cells except in the previously mentioned cell-free parts, the caudal portion of telencephalon in a 2 mm. longer larva is cell-free along the greater part of its surface. Commissura anterior as well as the pallial commissure are already developed at this latter stage. Although the cells are already ventricularly disposed in these small larvae throughout the greater part of the telencephalon, the embryonic brain differs from that of the adult in regard to the greater thickness of this cell-layer in the embryo. The brain walls are likewise thicker throughout in the larva.

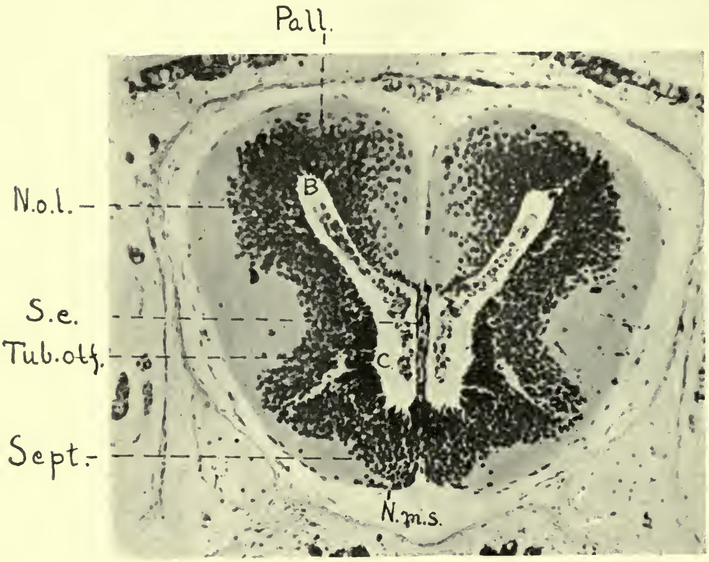

Fig. 28. Triton, about 2 cm. Cross section rostrally to foramen monroi. *N. m. s.*, nucleus medialis septi. *N. o. l.*, nucleus olfactorius lateralis. *Pall.*, pallium. *S. e.*, septum ependymale. *Sept.*, septal parts. *Tub. olf.*, tuberculum olfactorium.

The position of bulbus olfactorius remains lateral also in larvae of greater length. At stage 0,9 cm. nervus olfactorius thus enters bulbus in a purely lateral direction. No accessory bulbs are to be found in Triton. — Evagination is not so extensive in urodeles as in Anura. The lateral position of bulbus olfactorius is thus partly retained in the adult. There can therefore be no fusion between the bulbi of the two sides, the glomeruli-layer within bulbus never reaching the medial surface, as is the case in the frog.

Another consequence of the comparatively slight evagination of the brain is that the lateral ventricles are singularly short in proportion to the medial ventricle. Both the medial and the lateral ventricles are at stage 0,9 cm. very wide and open, it is only furthest frontad towards bulbus olfactorius that the lateral ventricles are narrow, vertically-directed fissures. It is here that the subpallial septum attains its greatest thickness; in Triton as in the frog, it is this part of telencephalon which developes latest. The medial septum nucleus forms first, developing in the medio-ventral anterior portion of the brain and then growing in a caudal direction. Nucleus lateralis septi originates in the caudal part of septum close to the ventricle, corresponding to its position in Rana, but is here comparatively small. Pars fimbrialis septi developes late and consists then exclusively of cells from the lateral nucleus. The entire septum is far less well developed in Triton than in the frog, as pallium in consequence of exceedingly vigorous inversion, stretches far down towards the ventral side, resulting in the septum parts only forming a smaller portion of the medial wall of the brain. The medial boundary between pallium and subpallium may be distinguished at the same time as the septal parts begin to become thicker; sulcus limitans internus is already clearly visible at an early stage; the medial boundary-zone begins to form almost simultaneously with the latter.

THE FOREBRAIN OF THE ADULT TRITON.

It appears from the above description of the embryonic development of the forebrain in Triton, that its main features agree well with those of the forebrain of the frog. These two types of brain are, however, distinguished from each other 1) by the more clearly demonstrated appearance of the transitory nuclei in anuran larvae and 2) by the varying degrees of evagination and inversion they undergo. The brain of the frog is the more differentiated, evagination proceeds more rapidly and embraces a larger portion of the telencephalon. A comparison of the position of bulbus olfactorius in these two groups of animals shows that even in the adult Triton it retains its embryonic situation on the lateral side of the hemisphere as mentioned above, while in Rana it occupies a fully rostral position with the exception of the small accessory bulb. In Triton the rostral epithelial membrane remains as a medial septum between the lateral ventricles in front of foramen monroi. The lateral ventricles are, as has already been pointed out, shorter in proportion to the medial ventricle than is the case in Rana, and never undergo such important transformation as in the latter. These types of brain differ also in regard to inversion, which in Triton is most extensive where the pallium in the adult individual stretches more than halfway down towards the ventral side, causing the pallial boundary to lie very far down on the medial wall. In the frog the subpallial part of the medial wall is, at least in the caudal portion of the hemisphere, considerably more extensive than in the pallial.

In the embryonic stages of Triton we recognize the same grooves as in the frog-larvae. With the assistance of these grooves and the tracts running outside the ventricular cell-layer, it is not difficult to homologize the different parts of telencephalon in these animals. The two pallial boundary-grooves have already been mentioned at the larval stages. The medial sulcus limitans internus may easily be traced through all stages. The sulcus limitans pallii is at times difficult to distinguish in Triton embryons during the process of development. In Triton as in the frog, the pallium extends along the ventricular wall to this groove, outwardly it is bounded by the dorso-lateral cell-free area. In the frog this cell-free area is further separated from the pallium by an outer groove, sulcus endorhinalis, which it has not been possible to discover in the Triton. The cell-free area is formed by the development of the lateral olfactory tract, the position of which can without difficulty be determined in the full-grown Triton. In fibre-impregnations of Triton and Salamandra this tract is found, not as in the frog, in the lateral wall of the brain, but dorsal to the ventricle. Thus the pallial boundary lies medially to this tract in urodeles. Considering the extremely vigorous inversion that the urodelebrain has undergone, it is not surprising that this pallial boundary is to be found in a dorsal position, pallium here lying in the main turned in towards the medial side, the subpallial parts of the lateral wall therefore also take a more dorsal position than in Anura. In the rostral part of the hemisphere the boundary runs between pallium and subpallium somewhat medially to the groove forming the dorso-lateral angle of the ventricle, further caudad it occupies a continually more lateral position till in the caudal portion of telencephalon it runs exactly in the above-mentioned angle.

In Tritons it is only possible to point out two separate parts in the pallium. Firstly, a medial part, corresponding to the hippocampal pallium, which is composed of cells similar to those described in this part of the frog, they are larger than the remaining pallium-cells and lie rather sparsely disposed between the ventricle and the surface of the brain; secondly, a dorsal part, where the cells are more closely packed towards the ventricle, from which they emanate radially. Between these two parts, which are separated by a distinct groove, sulcus limitans hippocampi lateralis, the cells in the outer part of the pallium are seen particularly compactly massed and forming an area separated from the medial as well as from the lateral portion of the pallium. It is possible that we have here the third part of the pallium, viz. the general pallium. The part situated nearest sulcus limitans pallii is homologous to the pyriformal pallium. — In the pallial part in Salamandra (fig. 29) these three parts are distinctly separated from each other. There we find medially two pallium parts, ventrally hippocampal pallium (*H. p.*), and dorsal to the latter, separated from it by sulcus limitans hippocampi lateralis, the general pallium (*G. p.*), extending to the dorso-medial corner of the ventricle. In Salamandra the cells in the general pallium are the largest; similarly to those in the hippocampal part, they extend as far as the surface of the brain.

Laterally to sulcus limitans pallii lies nucleus olfactorius lateralis, stretching round the dorso-lateral corner of the ventricle down the lateral side, where it is bounded by sulcus limitans externus. Ventral to the latter lies tuberculum olfactorium. During the embryonic stages the striatum never attains the powerful development that it undergoes in the frog-larvae, although even in the Triton-larvae it is larger and more fully developed than in the adult. Thus during the greater part of development the lateral walls, in this case also, undergo vigorous reduction, through which the originally rather compact ventricular cell-mass becomes extremely thin when the animal is full-grown. While in the frog these striatum parts extend right down to the under-lip of the ventricle, in Tritons the boundary between striatum and the medial parts lies dorsal to the same (fig. 28). The boundary between the ventral portion of the striatum and the medial parts of subpallium is formed by a groove, marked *C* at the larval stages, which is particularly distinct in the medial ventricle. Outside the lateral olfactory nucleus runs tractus olfactorius lateralis, while tuberculum olfactorium is situated within the lateral forebrain tract. The medial forebrain tract, which in Anura runs medial to the ventricle, is in the majority of urodeles situated ventral to the same.

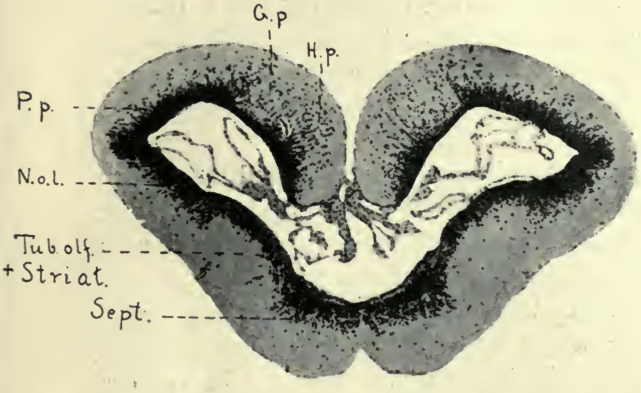

Fig. 29. Salamandra, adult. *G. p.*, general pallium. *H. p.*, hippocampal pallium. *N. o. l.*, nucleus olfactorius lateralis. *P. p.*, pyriformal pallium. *Sept.*, septal parts. *Striat.*, striatum. *Tub. olf.*, tuberculum olfactorium.

In the rostral portion of the hemisphere nucleus olfactorius lateralis is connected with a nucleus situated on the medial side of the lateral ventricle, this is the nucleus described by Herrick under the name of nucleus olfactorius anterior. Herrick also mentions that this nucleus is connected with the cell-part situated dorsal to the ventricle, a cell-part assigned by him to the pallium, but which is here referred to the nucleus olfactorius lateralis. This medially situated nucleus olfactorius is clearly homologous with the nucleus olfactorius medialis (eminentia postolfactoria, Gaupp), described in Anura, and which in the latter is the medial continuation of the lateral olfactory nucleus. In place of this nucleus, Herrick has pointed out as a homologon to the eminentia postolfactoria of frogs, a ventro-medially situated cell-part, calling it nucleus postolfactorius, and suggests the possibility of this part being homologous with the tuberculum olfactorium of mammals. This ventro-medial cell-part appears to form only the most rostral portion of septum, which here as in Anura borders on the ventral granular cells.

Ventral to nucleus olfactorius lateralis lies tuberculum olfactorium. While, in the larva, the latter is a fairly powerful cell-part, situated along the greater part of the lateral wall, in the full-grown Triton it is reduced to a narrow ventricular cell-layer, surrounding the lateral forebrain tract in the form of an arch. The hind part of tuberculum olfactorium becomes concentrated into a separate nucleus, nucleus tæniæ, situated caudal to foramen monroi.

The striatum situated within nucleus olfactorius lateralis and tuberculum olfactorium consists in Triton, as in the frog at the larval stages, of a rather compact ventricular cell-layer, divided by sulcus limitans externus into a dorsal and a ventral portion, which becomes reduced during embryonic development. That part of striatum which answers to the posterior portion of nucleus ventralis striatici is much less fully developed in urodeles than in Anura, a fact pointed out by HERRICK in describing the amygdala in Urodela.

In consequence of the slight degree of evagination undergone by the urodelebrain, the septum section proper forms only a small portion of the telencephalon. The ventricular part of the septum extends somewhat lateral to the ventral lip of the ventricle, where it is bounded partly by the above-mentioned groove (fig. 28, *C*), partly by an ependymal thickening corresponding with the ventral floor groove in Rana and with an ependymal cell-mass found there. The groove continues behind foramen monroi, where it forms the boundary between the medial and lateral portions of subpallium. Contrary to BINDEWALD, but in agreement with RÖTHIG, I have had no difficulty in distinguishing both a lateral and a medial septum nucleus in urodeles as well, although they are inferior in size to the powerful septal nuclei in Anura. The origin of the two nuclei is exactly similar to that in Rana, and as in Anura they also in Urodela form the fimbrial part of septum.

SUMMARY.

1. From a phylogenetic point of view the ventricular disposition of cells in the amphibian brain cannot be said to be of a primary nature.

2. The lack of differentiated cortices in telencephalon is probably a secondary manifestation, as we find in the larvae, clearly separated from the inner ventricular layer, a migrated cell-layer representing the cerebral cortex, which later is again forced in towards the ventricle. Thus the ventricular cell-layer in the adult Amphibia corresponds in general with the ventricular layer in the larvae as well as with their migrated cerebral cortex. The hippocampal

pallium, however, forms an exception in this respect, its migrated cortical parts being diffusely spread over the corresponding portion of the ventricular wall.

3. The boundary between the pallial and subpallial parts should, on the lateral side, be drawn dorsally to the wall-region whose lower part forms regio curva, i. e. the lobus pyriformis of the authors. Thus the lateral olfactory tract will run through the subpallial part of the brain in amphibians as well as in the lower vertebrates. Medially we find a distinct zona limitans; the septal nuclei situated ventrally to the latter and forming the fimbrial parts, are always of subpallial origin.

4. In the pallium we recognize the cortical parts characteristic for vertebrates in general; viz.: the hippocampal pallium, the general pallium and the pyriform pallium.

5. There is no trace of a hypopallial ridge (epistriatum).

6. Ventral to the lateral boundary groove of the pallium, sulcus limitans pallii, in the larva is found, firstly an inner ventricular part, striatum, divided by sulcus limitans externus into a dorsal and a ventral portion; secondly, an outer part consisting dorsally of nuclus olfactorius lateralis, and ventrally of tuberculum olfactorium. These outer portions are later forced back towards the ventricle; thus in the adult Amphibian the ventricular part in subpallium answers dorsally to nucleus olfactorius lateralis as well as to striatum (nucleus dorsalis) and ventrally to tuberculum olfactorium and striatum (nucleus ventralis). Nucleus olfactorius lateralis continues rostrad and mediad as nucleus olfactorius medialis (eminentia postolfactoria, Gaupp). Caudally tuberculum forms a detached nucleus, nucleus tæniæ.

7. In addition to the ventricular cell area two nuclei are found in the septum, nucleus medialis septi, forming a continuation of the granular cells of bulbus olfactorius, and nucleus lateralis septi, which developes immediately below zona limitans medialis close to the wall of the ventricle, and is separated in a ventricular direction by sulcus septalis from the rest of the septum.

8. The pallial cortical parts and the subpallial migrated nuclei are never as well defined in the forebrain of urodele-larvae as in Anura. This brain is therefore never exposed to such a radical process of reduction in the pallial and striatal parts, these less clearly defined cell-areas being already at an early stage forced in towards the ventricle. In regard to evagination, it should be noticed that it does not in urodeles attain the same extension as in Anura, and that the pallial parts in urodeles are situated more dorsally and medially, and do not extend on the lateral side below the dorsal corner of the ventricle. The position of the subpallial parts on the lateral side becomes therefore more dorsal than that of corresponding parts in Anura.

The results summarized above seem to have some bearing on the question of the phylogenetic development of the forebrain in higher vertebrates, and to contribute to the understanding of the position of the amphibian forebrain in relation to that of the other vertebrates. The evidence for the forebrain of amphibians being a highly reduced one, undoubtedly points to their ancestors having had a forebrain of higher differentiation. The fact that in the Pipa embryo the forebrain nuclei are developed as in reptiles with the exception of the non-existant hypopallial ridge makes it probable that the common ancestors of Amphibians and reptiles were, in regard to the morphology of the forebrain, developed in a manner that made evolution possible in an amphibian direction on the one hand and in a reptilian on the other. This conclusion enables us to sketch the main structure of the Stegocephalian forebrain. This brain may have been evaginated, the pallial parts may have had a pallial cortex independent of the ventricular layer and probably subdivided into the three characteristic parts. No ventricular (hypopallial) ridge existed. In the subpallial part the corpus striatum together with a nucleus dorsalis and a nucleus ventralis was developed. In addition to these, there was a nucleus olfactorius lateralis, a well developed tuberculum olfactorium and the two septal nuclei. A fimbrial part probably also existed. This view is based partly on the conditions in reptiles, partly on those in lower vertebrates, where, e. g. in sharks, the same parts are ontogenetically present. The formation of the hypopallial ridge belongs to a later phylogenetic stage. As this ridge is found in turtles as well as in all other reptiles, but not in the lower vertebrates, it is very probable that this structure originated in the ancestral group of reptiles viz.: in the Cotylosauria.

In the Anura the ontogenetical appearance of the transitory nuclei is more clearly manifested than in the urodeles. From this fact the conclusion may be drawn that the anuran forebrain corresponds more closely to that of the stegocephalians than to that of the urodeles. These two groups may have followed different lines of development. In the urodeles reduction of the forebrain nuclei may have taken place at an earlier period than in the Anura, in consequence of the differentiation of the transitory nuclei being less pronounced.

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